# TROPHIC ECOLOGY AND FOOD WEB MODELLING OF MID-SLOPE DEMERSAL FISHES OFF SOUTHERN TASMANIA, AUSTRALIA

by

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*The owl and the pussy cat went to sea . . .*

## DECLARATION AND AUTHORITY OF ACCESS

I hereby declare that the material in this thesis is original except where due acknowledgement is given, and that the material has not been accepted for the award of any other degree or diploma.

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C M Bulman

# ABSTRACT

The trophic ecology and food web dynamics of the mid-slope demersal fish community (700-1200 m) off southern Tasmania were investigated. The top predators in the community were orange roughy, the oreos and squalids. Orange roughy *Hoplostethus atlanticus* is dominant on the flat ground but even more so on the seamounts, and consequently fishing has been intense on these seamounts. Oreos are also fished on the seamounts. During 10 research cruises around south-eastern Australia, more than 9000 stomachs from orange roughy and 23 other species were collected and examined. Orange roughy ate predominantly mesopelagic and benthopelagic fish, crustaceans and squid as adults, and mainly crustaceans as juveniles suggesting resource partitioning between juveniles and adults. Orange roughy, warty dory *Allocyttus verrucosus*, squalids and macrourids are benthopelagic omnivores. In contrast, the smooth oreo *Pseudocyttus maculatus*, and the alepocephalids ate pyrosomes.

Daily rates of food consumption for adult orange roughy were 1.15% body weight and for juveniles were 0.91%. The metabolism of orange roughy estimated from a mass balance model, was similar to that of active, migratory mesopelagic fishes and greater than non-migratory bathypelagic fishes. The use of enzyme activity rates of white muscle as proxies for oxygen consumption was investigated for orange roughy and seven other dominant species in the community. Lactate dehydrogenase (LDH), malate dehydrogenase (MDH) & citrate synthase (CS) activities were assayed. The fishes were all anaerobically poised, with LDH activities greater than CS activities. The LDH activities of smooth oreo, dogfish *Centroscymnus crepidater* and orange roughy were higher than the majority of deep-living species studied previously. The oxygen consumption rate for orange roughy, estimated from the bioenergetic model, was best estimated from LDH activities. Oxygen consumption for the seamount-associated fish similar to orange roughy, might also be best predicted from LDH activities.

Food web models using Ecopath with Ecosim models were developed to examine scenarios of fishing impacts and pelagic inputs to the community through advection. Diet composition, species composition, biological and physiological parameters for each food web group, collected from the research cruises, as well as

fishery catch statistics, were used in construction of the models. After simulating a decade of fishing, orange roughy declined to about 60% of the starting biomass but recovered to 99% of starting biomass over the next 40 years once fishing ceased. The oreos declined more and only recovered to 57% once fishing ceased. Advection of prey was the most important mechanism by which the community biomass on the seamounts could be sustained. High rates allowed the orange roughy stocks to recover in less than 20 years and oreos in 55 years while low advection rates would allow recovery to only two-thirds pre-fishing biomass for both fisheries.

# ACKNOWLEDGEMENTS

This thesis is the result of work I have completed while working at CSIRO Marine Research. This work was part of a larger study of the mid-slope ecosystem off southern Tasmania and involved many people, each of whom were responsible for various parts of the project. My part was the demersal fish community. This project entailed working at sea with other team members, all of who contributed in various ways to helping me to complete this work and to whom I am very grateful. The papers embodied in this thesis are the results of my research. They are either published or in the process of being published. Co-authors have generally played a supervisory role and are duly acknowledged.

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# CONTENTS

# CHAPTER 1

## GENERAL INTRODUCTION

# Introduction

The deep-sea is an extreme environment that is immensely difficult to explore. Any creatures living there are subjected not only to cold, dark and high pressure but also a sparse and patchy food supply. For human investigators, these conditions are even more difficult to overcome except with the aid of cumbersome and expensive equipment. We must usually work from the unstable platform of a ship, in an environment that may be severely affected by weather conditions. Furthermore our sampling devices e.g. fishing nets, water sampling gear, bottom sampling dredges, cameras or acoustic sounders may be operating up to several kilometres from the ship, making precise sampling miraculous, if achievable at all. Despite the difficulties that these conditions present to investigators, the deep-sea has been sporadically explored for over 100 years (Merrett and Haedrich 1997).

More recently however, the expanding need for food has accelerated the exploitation of deep-sea resources before a clear understanding of the ecology of these species has been established. The discovery and subsequent exploitation of a large fishable resource of orange roughy (*Hoplostethus atlanticus* Collett) on the mid-slope around south-eastern Australia and New Zealand in the late 1970s highlighted our lack of knowledge of this species and other co-habitants of the mid-slope community. Management of single-species fisheries in isolation from their supporting ecosystems has not been particularly successful, as witness the collapse of many northern hemisphere fisheries. Recognition that a multi-species approach might prove better has since gained strength.

*Orange roughy and the Australian South East Fishery*

In Australia, orange roughy is now one of the prime commercial species of the South East Fishery (SEF). The fishery occupies that part of Australia's Exclusive Economic Zone (EEZ) from 3-200 n miles offshore and from 138° 08' E, east of Cape Jervis in South Australia, to 33°35' S, south of Barrranjoey Pt in New South Wales (Fig 1). It contains 15 commercially exploited species of fish and 1 crustacean, all of which are managed by the Commonwealth of Australia,

specifically the Australian Fisheries Management Authority (AFMA). The orange roughy fishery on the mid-continental slope (700-1200 m) was first exploited in the early 1980s and rapidly became one of Australia's most valuable fisheries. In 1992, it was worth $46.7 million and accounted for 62% of the whole SEF trawl fishery (Chesson 1996), but it has since declined to $14.4 million and 22% of the total in 1999, (including the landings from the Cascade Plateau and Remote Zone) (Smith & Wayte 2001). At the peak of the fishery in 1990, orange roughy landings were about 75% of the total landed catch in the SEF (Chesson 1996). Up to and including 1999, a total of about 171 001 tonnes were officially reported from the SEF, of which 67 740 tonnes (~40%) were from an area south of Tasmania largely covered by seamounts (Smith & Wayte 2001). However, the best estimate of actual landings was 223 570 tonnes (Smith & Wayte 2001), the difference being due to misreporting over a period of years.

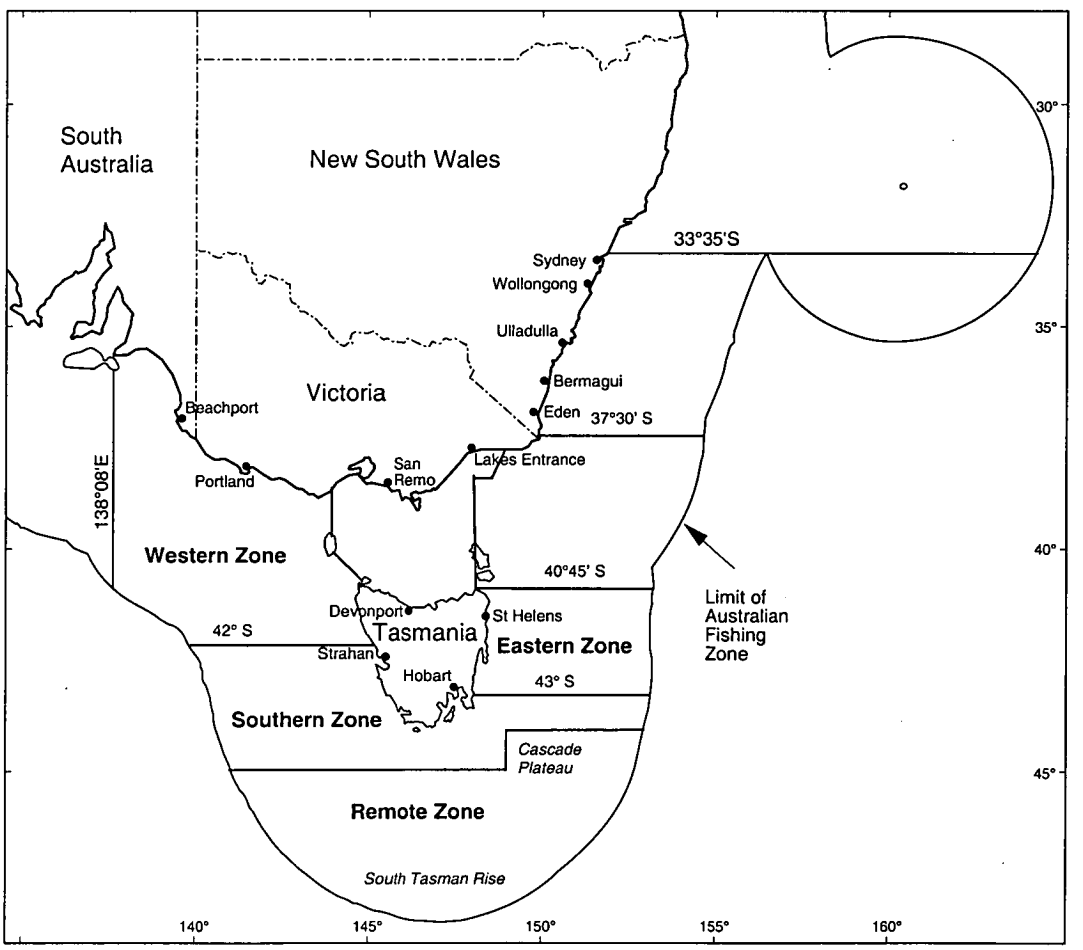


**Fig 1.** The South East Fishery management region off south-eastern Australia.

*The Southern Zone Orange Roughy Fishery*

From 1990, the area south of Tasmania (later to become the Southern Management Zone) became the focus of the orange roughy fishery when large non-spawning aggregations were discovered on its seamounts. A large spawning aggregation was also discovered off the east coast of Tasmania. Even now it is unclear whether these two areas hold separate stocks of orange roughy. Otolith shape suggests that the non-spawning southern zone fish are similar to the east coast spawners, however they are distinct from the eastern non-spawning fish and the southern 'winter-caught' stock (Wayte and Bax 2001). Trawling had until then been on flat bottom, but fishers rapidly developed fishing skills to trawl the rough ground and seamounts. In 1990, nearly 25 000 tonnes of roughy were landed from the southern area. To restrict the rapid expansion of this fishery, management zones and total allowable catches (TACs) were introduced in 1992. By 1993, a total of nearly 60 000 tonnes of roughy had been landed from the Southern Zone (Smith & Wayte 2000). In the following year, the TAC was halved to 5000 tonnes and finally reduced to 700 tonnes in 1999 and 2000 (Wayte and Bax 2001). Introduction of these catch limits reduced the proportion of orange roughy in the total SEF landings to about 31% in 1994 and 15% in 1999 (Wayte and Bax 2001). Recently, landings from remote zones on the South Tasmania Rise and Cascade Plateau, areas that probably hold separate stocks and are similarly vulnerable to over-fishing, have grown substantially.

Although the demersal fish community in the SEF is dominated by orange roughy (Koslow *et al.* 1994), representatives of other families including Oreosomatidae, Squalidae, Macrouridae and Alepocephalidae, comprise the majority of the fish community (Koslow *et al.* 1994). Since the introduction of an orange roughy quota, some of these species are now targeted for commercial fishing. The landings of smooth oreo *Pseudocyttus maculatus* and spikey oreo *Neocyttus rhomboidalis* have varied between 2449 tonnes and 744 tonnes respectively in 1992 to 1297 tonnes and 428 tonnes respectively in 1998 (Chesson 1996, Smith & Wayte 2000). The values of these fisheries were $1.2 million and $0.3 million respectively in 1998 (Chesson 1996, Smith & Wayte 2000). Dogfishes *Centroscymnus* species and *Deania calcea*, have also been fished, and about 1000 tonnes of whole fish,

worth between $0.75–1 million, were landed in 1999 from the SEF, of which about half was caught off western Tasmania (Daley *et al.* 2001).

Recent stock assessments have indicated that the biomass in the Southern Zone is probably less than 20% of the virgin biomass and that even a zero TAC may be unable to achieve management targets, i.e. to rebuild stocks to 30% virgin biomass (Wayte and Bax 2001). No estimates of biomass for Australian stocks of any oreo have been made and little new information has been acquired to assist management of these stocks. In 1992, the fishery for smooth and black oreos was considered under-exploited (Lyle *et al.* 1992), however subsequent expansion of the fishery may now threaten that assumption. The dogfish fishery also expanded quickly since 1992 and, despite its relatively small size, current knowledge indicates that these species may also be over-exploited (Daley *et al.* 2001).

*Orange Roughy surveys*

In 1988-89, after the initial flurry of activity and before the height of the orange roughy boom in the Southern Zone, CSIRO Division of Fisheries attempted to assess the relative abundance of orange roughy in the SEF by trawl survey. At the time, there were no estimates of abundance and very few biological data on roughy. Fishing at this depth was relatively new in Australia and few boats had the capability to trawl at 1000m or greater. Random trawl surveys were conducted from the CSIRO's FRV *Soela* (Bulman *et al.* 1994). Smooth, fishable ground was surveyed from 700-1200m from Point Hicks in South Australia, around Tasmania and to Gabo Island off NSW.

Trawl survey estimates were later shown to grossly underestimate the biomass of roughy because, at the time of the surveys, the majority of fish lived undetected on seamounts that were considered unfishable and so were not included in the surveys. However, the surveys provided at least some of the samples for ageing (Fenton *et al.* 1991), reproduction (Bell *et al.* 1992, Koslow et *al.* 1995) and dietary analyses (Chapter 2, Bulman and Koslow 1992). The results of these analyses identified orange roughy as an unusual deep-sea fish because they are slow-growing and long-lived and appear to have relatively high metabolic rates compared to other deep-sea fishes. Orange roughy is estimated to live to over 125-140 years based on radiometric aging of otoliths and mature quite late (~25 years) (Fenton *et al.* 1991,

Smith *et al.* 1995). Estimates of the von Bertalanffy growth parameter, K, for Australian fish vary between 0.06 (Tilzey 1994) and 0.044 (Fenton *et al.* 1991), which is considered very low amongst fish species. Mortality estimates of 0.048 or 0.064,depending on the assumed age at full recruitment –31 or 40 years respectively– have been used in Australian stock assessments (Smith *et al.* 1995). Fecundity estimates of orange roughy are low, between 20 000–49 000 eggs per kg (Pankhurst and Conroy 1987, Clark *et al.* 1994, Bell *et al.* 1992, Koslow *et al.* 1995). Their unusual biology makes them vulnerable to over-fishing thus further research was warranted.

The oreos have similar life-history parameters to orange roughy and must also be at risk from over-exploitation (Lyle *et al.* 1992). The smooth oreo *Pseudocyttus maculatus* and black oreo *Allocyttus niger*, are similarly long-lived, mature late (~31 years) and have low fecundities (10 800 and 17 500 eggs per kg) (Stewart *et al.* 1995, Conroy and Pankhurst 1989, Doonan *et al.* 2001). No mortality estimates for Australian oreos are available but biomass estimates of New Zealand smooth oreo used mortality estimates of 0.063 and *k* estimates of 0.047 and 0.067 (Doonan *et al.* 2001), very similar to those for orange roughy.

*Southern Zone Trophodynamic Project*

In 1990, CSIRO Division of Fisheries (now CSIRO Marine Research) designed a study to improve the understanding of the ecology of the deep-water fish stocks, particularly orange roughy, on the mid-slope (Parslow *et al.* 1996). It was designed specifically to describe the food chain supporting the fish stocks and their dependence on oceanographic events at a study site off the Tasmanian south coast. The site was situated south of Pedra Branca where the commercial fishers have caught large catches of adult non-reproductive orange roughy. The region may be an important holding area or it may be poor in feeding opportunities causing the poor condition and non-reproductive status of these fish. Zooplankton, nekton, and the demersal fishes were sampled at the study site.

The oceanography of the area is complex (Harris *et al.* 1991, Parslow *et al.* 1996) and only a summary is given here. The waters around Tasmania are part of the Subtropical Convergence Zone (Harris *et al.* 1991). There is a temperate seasonal cycle and interannual variability. On the east coast, a warm saline current, an

extension of the East Australian Current, flows south. On the west coast, warm saline water known as the Zeehan current, flows south. Both therefore influence the deep currents on the slope south of Tasmania. Over the series of 4 cruises, measurements of physical, chemical and biological variables of the water column were made along three transects across the shelf and down the slope and are reported in Parslow *et al.* (1996).

*Objectives of this study*

At this time, the trophic structure of the mid-slope community off southern Australia was largely unknown. Diets of commercial fish species had been studied from the shelf areas off Victoria in the early 1980s (Coleman & Mobley 1984) and from the Tasmanian upper slope demersal community, dominated by blue grenadier *Macruronus novaezelandiae,* and the pelagic community, which was dominated by *Lampanyctodes hectoris* (Bulman & Blaber 1986, Blaber & Bulman 1987, Young & Blaber 1986). On the New Zealand mid-slope, the diets of a number of the members of the community have been described, including those of orange roughy and oreos (Rosecchi *et al* 1991, Clark *et al.* 1989). The diets of fish from the mid- and upper-slope of the eastern North Atlantic Ocean, the western North Atlantic Ocean, and off Oregon in the northeast Pacific Ocean, and off the South African continent have also been well studied. However, in Australia, little was known of the structure and functioning of the community that supported one of the country's most valuable fisheries. This thesis aims to fill some of these gaps. The following chapters are in the form of published or submitted papers, and each contains corresponding references. Consequently, there is an unavoidable repetition of some facts and figures and I beg the reader's indulgence.

In Chapter 2, I describe the diet of a large number of orange roughy from the broad surveys of the mid-slope of south-eastern Australia. From this detailed dietary study, evacuation rates and daily ration are calculated and a simple bioenergetic model for orange roughy is derived. From the model, the metabolic rate of orange roughy is estimated.

In Chapter 3, I investigate the trophic structure of the mid-slope community from a small site off the south coast of Tasmania. I describe the diets of orange roughy and the other dominant fish species. They are compared to the same or

similar species from other dietary studies from comparable ecosystems. The trophic structure of the demersal food web is outlined and trophic level assignments are made for each species or species group in the web. The aim was to provide a preliminary framework on which to build a trophic model of the demersal ecosystem.

In Chapter 4, I investigate the metabolic requirements of eight dominant members of the community, by using proxy indicators–metabolic enzyme activities of white muscle. These enzymes have been useful in estimating metabolism for some species and I examine some relationships. The field estimate of orange roughy oxygen consumption is compared with an enzyme derived estimate. Also I make inferences about activity levels and ecology of the species of the mid-slope community, drawn from the measured enzyme activities.

In Chapter 5, I model the community using the ecological software, Ecopath with Ecosim (EwE) (Christensen *et al.* 2000). Because the models are intended to describe "average " states, several models were developed. Firstly, a model was developed for the community on the flat grounds where roughy is more dispersed and another for the seamounts before the stocks were heavily fished. The effects of various rates of immigration of micronekton prey groups were investigated for the seamount model. Finally, actual fishing rates are simulated and corresponding changes to the system investigated.

In Chapter 6, I briefly summarise the results and conclusions, with reference to the objectives, which were:

1. to describe the trophodynamics of the demersal fish community of the mid-slope, in particular orange roughy and some other dominant species (Chapters 1 & 2),

2. to determine the significance of the contribution of prey from pelagic or other sources (chapter 1 & 2),

3. to determine the energy requirements and make inferences about the activities of dominant fish species from dietary and metabolic studies (chapter 3), and

4. to model the trophic structure of the mid-slope community to determine the levels of production required to sustain the demersal fish community pre-fishing and reconstruct the effect of fishing on the community (chapter 4).

## References


**Bell, J. D., Lyle, J. M., Bulman, C. M., Graham, K. J., Newton, G. M., and Smith, D. C.** (1992). Spatial variation in reproduction, and occurrence of non-reproductive adults, in orange roughy, *Hoplostethus atlanticus* Collett (Trachichthyidae), from south-eastern Australia. *Journal of Fish Biology* **40**, 107-122.

**Blaber, S. J. M., and Bulman, C. M.** (1987). Diets of fishes of the upper continental slope of eastern Tasmania: content, calorific, values, dietary overlap and trophic relationships. *Marine Biology* **95**, 345-356.

**Bulman, C. M. and Blaber, S. J. M.** (1986). The feeding ecology of *Macruronus novaezelandiae* (Hector 1871) (Teleostei: Merluciidae) in south-east Australia. *Australian Journal of Marine and Freshwater Research* **37**, 621-639.

**Bulman, C. M. and Koslow, J. A.** (1992). Diet and food consumption of a deep-sea fish, orange roughy *Hoplostethus atlanticus* (Pisces: Trachichthyidae), off southeastern Australia. *Marine Ecology Progress Series* **82**, 119-125.

**Bulman, C. M., Wayte, S. E. and Elliott, N.** (1994). Abundance and distribution of orange roughy 1988-89. *CSIRO Marine Laboratories Report* **215**.

**Chesson, J.** (ed) (1996). The South East Fishery 1995. Fishery Assessment Report compiled by the South East Fishery Assessment Group. (Australian Fisheries Management Authority, Canberra.)

**Christensen, V., Walters, C. & Pauly, D.** (2000). Ecopath with Ecosim: A User's Guide. (Fisheries Centre, University of British Columbia, Vancouver, Canada and ICLARM, Penang, Malaysia.) 130 pp.

**Clark, M. R., Fincham, D. J., and Tracey, D. M.** (1994). Fecundity of orange roughy (*Hoplostethus atlanticus*) in New Zealand waters. *New Zealand Journal of Marine and Freshwater Research* **28**, 193-200.

**Clark, M. R., King, K. J., and McMillan, P. J.** (1989). The food and feeding relationships of black oreo, *Allocyttus niger*, smooth oreo, *Pseudocyttus maculatus*, and eight other fish species from the continental slope of the south-west Chatham Rise, New Zealand. *Journal of Fish Biology* **35**, 465-484.

**Coleman, N., and Mobley, M.** (1984). Diets of commercially exploited fish from Bass Strait and adjacent Victorian Waters, south-eastern Australia. *Australian Journal of Marine and Freshwater Research* **35**, 549-60.

**Conroy, A. M. and Pankhurst, N. W.** (1989). Size-fecundity estimates in the smooth oreo, *Pseudocyttus maculatus*, and the black oreo, *Allocyttus niger* (Pisces: Oreosomatidae). *New Zealand Journal of Marine and Freshwater Research* **23**, 525-527.

**Daley, R., Stevens, J. and Graham, K.** (2001). Catch analysis and productivity of the deepwater dogfish in southern Australia. Final Report to Fisheries Research and Development Corporation. FRDC Project 98/105.

**Doonan, I. J., McMillan, P. J., Coburn, R. P. and Hart, A. C.** (2001). Assessment of OEO4 smooth oreo for 2000-01. New Zealand Fisheries Assessment Report 2001/21. (NZ Ministry of Agriculture and Fisheries, Wellington). 37 pp.

**Fenton, G. E., Short, S. A. and Ritz, D. A.** (1991). Age determination of orange roughy *Hoplostethus atlanticus* (Pisces: Trachichthyidae), using 210 Pb/226 Ra disequilibria. *Marine Biology* **109**, 197-202.

**Harris, G. P., Griffiths, F. B., Clementson, L. A., Lyne, V., and Van der Doe, H.** (1991). Seasonal and interannual variability in physical processes, nutrient cycling and the structure of the food chain in Tasmanian shelf waters. *Journal of Plankton Research* **13** Supplement, 109-131.

**Koslow, A. J., Bulman, C. M., Lyle, J. M.** (1994). The mid-slope demersal fish community off southeastern Australia. *Deep-Sea Research* **41**, 113-141.

**Koslow, J. A., Bell, J., Virtue, P., and Smith, D. C.** (1995). Fecundity and its variability in orange roughy: effects if population density, condition, egg size, and senescence. *Journal of Fish Biology* **47**, 1063-1080.

**Lyle, J., Riley, S. and Kitchener, J.** (1992). Oreos–an underutilised resource. *Australian Fisheries* **54**, 12-15.

**Merrett, N. R. and Haedrich, R. L.** (1997). Deep-sea demersal fish and fisheries. (Chapman & Hall, London.) 282 pp.

**Pankhurst, N. W. and Conroy, A. M.** (1987). Size-fecundity relationships in the orange roughy, *Hoplostethus atlanticus*. *New Zealand Journal of Marine and Freshwater Research* **21**, 295-300.

**Parslow, J., Koslow, J. A., Griffiths, F. B., Clementson, L., Rathbone, C., Bonham, P., and McKenzie, D.** (1996). Tasmanian Slope Trophodynamics Final Report **96**. (CSIRO Division of Fisheries, Hobart, Tasmania.)

**Rosecchi, E., Tracey, D. M., and Webber, W. R.** (1991). Diet of orange roughy, *Hoplostethus atlanticus* (Pisces: Trachichthyidae) on the Challenger Plateau, New Zealand. *Marine Biology* **99**, 293-306.

**Smith, D. C., Fenton, G. E., Robertson, S. G., Short, S. A.** (1995). Age determination and growth of orange roughy (*Hoplostethus atlanticus*): a comparison of annulus counts with radiometric ageing. *Canadian Journal of Fisheries and Aquatic Sciences* **52**, 391-401.

**Smith, A. D. J. and Wayte, S. E.** (eds) (2000). The South East Fishery 1999. Fishery Assessment Report compiled by the South East Fishery Assessment Group. (Australian Fisheries Management Authority, Canberra.)

**Smith, A. D. J. and Wayte, S. E.** (eds) (2001). The South East Fishery 2000. Fishery Assessment Report compiled by the South East Fishery Assessment Group. (Australian Fisheries Management Authority, Canberra.)

**Stewart, B. D., Fenton, G. E., Smith, D. C. and Short, S. A.** (1995). Validation of otolith-increment age estimates for a deepwater fish species, the warty dory, Allocyttus verrucosus, by radiometric analysis. *Marine Biology* **123**, 29-38.

**Tilzey, R.** (1994). The South East Fishery. Fishery Assessment Report compiled by the South East Fishery Assessment Group. (Australian Fisheries Management Authority, Canberra.)

**Wayte, S. and Bax, N.** (2001). Orange Roughy (*Hoplostethus atlanticus*). Stock Assessment Report 2001. Compiled for the South East Fishery Stock Assessment Group. (Australian Fisheries Management Authority, Canberra.)

**Young, J. W. and Blaber, S. J. M.** (1986). Feeding ecology of three species of midwater fishes associated with the continental slope of eastern Tasmania. *Marine Biology* ***93***, 147-156.

# CHAPTER 2

## Diet and food consumption of a deep-sea fish, orange roughy, *Hoplostethus atlanticus* (Pisces: Trachichthyidae) from southeastern Australian waters.

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# Diet and food consumption of a deep-sea fish, orange roughy *Hoplostethus atlanticus* (Pisces: Trachichthyidae), off southeastern Australia

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ABSTRACT: We examined the diet of nearly 7500 orange roughy *Hoplostethus atlanticus* Collett, 1889 from southeastern Australian waters caught during trawl surveys in 1988 and 1989. Juveniles fed mainly on bentho- and meso-pelagic crustaceans, while mature fish consumed predominantly fish and squid. The composition of the diet changed significantly with depth, geographical area, and year. Evidence of diel feeding periodicity found in adults at a station sampled over 42 h was supported by patterns of stomach fullness and digestion stage in the full data set. Based upon observed rates of stomach evacuation, daily rates of food consumption were estimated as 1.15 % body weight for adults and 0.91 % for juveniles. The metabolism of orange roughy, estimated from a mass balance model, is similar to that of active, migratory mesopelagic fishes and substantially higher than that of non-migratory bathypelagic fishes. The bodily composition of orange roughy, which is high in lipid and protein and low in water, is also similar to that of active mesopelagic fishes. Non-migratory bathypelagic fishes typically have exceptionally low metabolic rates, which, despite low food consumption, lead to high growth rates and high growth efficiency. Orange roughy, however, appears to have very high metabolic costs, which lead to an exceptionally low growth rate and growth efficiency, despite relatively high rates of food consumption.

## INTRODUCTION

The food consumption and metabolism of deep-sea fishes have seldom been studied. There is particular interest in orange roughy *Hoplostethus atlanticus* Collett, 1889 because of the recent development of deepwater fisheries for this species off New Zealand and Australia. Orange roughy are found in the northeast Atlantic (Mauchline & Gordon 1984), around the southern coast of South Africa to Madagascar and on the West Australian ridge in the Indian Ocean (Kotlyar 1980, Smith & Heemstra 1986), but commercially significant quantities are not known from these regions. Studies in several parts of the world ocean (Kotlyar & Lipskaya 1980, Mauchline & Gordon 1984, Gordon & Duncan 1987, Rosecchi et al. 1988) show consistently that orange roughy feed on bentho- and mesopelagic crustaceans, fish and squid. Crustaceans predominate in the diet of small orange roughy, and their diet shifts to fish as they grow (Rosecchi et al. 1988). Orange roughy seems to be an opportunistic, generalized benthopelagic predator similar to other fish at these depths (Mauchline & Gordon 1986, Blaber & Bulman 1987).

The food consumption and metabolism of orange roughy have not been studied. The species has not been maintained under laboratory conditions, and Rosecchi et al. (1988) found no evidence of diel periodicity in feeding, from which digestion rates may be estimated using stomach-content data from the field (Eggers 1977, Clarke 1978). Bathypelagic organisms generally consume less food than shallower species, possibly because their metabolism is lower rather than due to decreased growth rate (Torres et al. 1979, Childress et al. 1980, Mauchline 1988). However, orange roughy grows very slowly: validated otolith-based and radiometric aging studies indicate that orange roughy matures at about 20 yr at ~ 30 cm, and grows only 15 to 20 cm further over a life-span of 50 to 100+ yr (Mace et al. 1990, Fenton et al. 1991). It might be expected, therefore, that orange roughy has a particularly low rate of food consumption, if its metabolism is similar to that of other non-migratory deepwater species.

Orange roughy is widely distributed in temperate Australian waters in depths from 700 to 1200 m, where it is often the dominant species (Bulman et al. in press). This study of orange roughy feeding is based upon a large collection of stomachs (at least 10-fold more than



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previous studies of orange roughy feeding) that was obtained in southeastern Australian waters over two 5 mo field seasons.

Our objectives in this study were: (1) to describe the diet of orange roughy in Australian waters in relation to area, depth, size, and year; and (2) to examine the food consumption and metabolism of orange roughy based upon an analysis of diel feeding periodicity and digestion rate.

## MATERIALS AND METHODS

**Field collection.** In 1988 and 1989, an area of about 13 000 km$^2$ off southeastern Australia was surveyed by FRV 'Soela', using an Engel high-lift trawl (Fig. 1). The survey was based on a random depth-stratified design consisting of 100 m depth strata from 700 to 1200 m in 1988 and 800 to 1200 m in 1989. Cruises were undertaken from January to May in both years. The number of valid stations at which orange roughy were caught was 162 in 1988 and 167 in 1989. The survey area was divided into subareas corresponding to broad geographical regions: Great Australian Bight (GAB), western Tasmania and western Bass Strait (WTas), eastern Tasmania (ETas), eastern Bass Strait (EBass), and in 1988, New South Wales (NSW) (Fig. 1). A site off NSW was sampled at regular intervals over 82 h to obtain data on diel feeding periodicity, but sufficient adult orange roughy were obtained only for the first 42 h.

**Laboratory analysis.** The stomachs of up to 40 orange roughy from each tow were examined in the 1988 survey and 20 per tow in the 1989 survey. The whole stomach was assessed for digestion as being either at an early (stage 1) or late (stage 2) stage of digestion. Prey items were identified to species or genus where possible, and weighed after excess moisture had been removed.

**Data analysis.** The numbers in many prey categories were too low to permit statistical analysis, so prey items were grouped into more general taxa [sergestids, pasiphaeids, oplophorids, mysids, amphipods, other Crustacea (mostly unidentified), fish, squid and other prey (miscellaneous)]. The percentage of the total weight of the prey and the frequency of occurrence of prey items in stomachs containing food were calculated for each prey category. Stomach fullness for each tow (g kg$^{-1}$) was calculated by dividing the summed weight of prey items in all the stomachs by the weight of all fish examined.

The data were analysed separately by subarea, depth, year, and length. In all analyses except by length, data from fish $> 30$ cm (the mean size at maturity) and fish $\leq 30$ cm were analysed separately. The number of tows in the EBass area in 1989 was too small to compare with the 1988 results and there were no NSW data in 1989. Consequently only data from GAB, WTas and ETas in both years were analysed. Data from tows within aggregations of orange roughy (i.e. large concentrations that were recognizable both acousti-

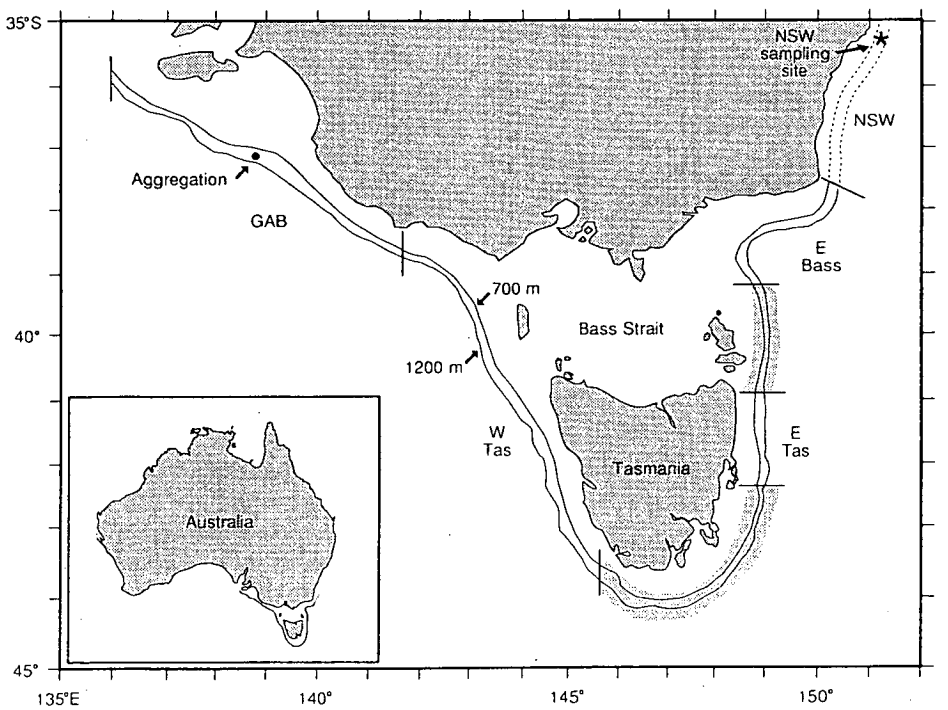


Fig. 1. Survey area off southeastern Australia showing the 700 and 1200 m depth contours, boundaries of the regional survey strata, and location of the orange roughy *Hoplostethus atlanticus* aggregation. The shaded areas represent untrawlable grounds, which were not surveyed. The NSW sampling station is indicated by ★. GAB = Great Australian Bight; WTas = West Tasmania and Bass Strait; ETas = East Tasmania; EBass = East Bass Strait; NSW = New South Wales

cally and from the trawls) were compared with data from the rest of the subarea.

The overall similarity of diets from different areas was tested with Kendall's coefficient of concordance, $W$ (Tate & Clelland 1957), a nonparametric ranking test and Friedman's rank 2-way classification, $T$ (Conover 1971). More detailed analyses of variation in diet in relation to fish size, depth, year, subarea, and aggregation were conducted with contingency-table analyses or logistic regression, based upon the frequency of occurrence of different prey items in the stomachs. The prey items were grouped into major sub-categories (crustaceans, fish, squid) in carrying out more complex statistical analyses.

Two types of data were used to investigate diel periodicity of feeding. Mean stomach fullness per tow and the proportions of stomachs at each digestion stage were each averaged per 4 h interval. Digestion stages 1 and 2 were combined because of low numbers in both stages, and stages 3 and 4 were combined, since both indicated late stages of digestion and were apparently reached many hours after intake. These data were plotted and contingency analyses carried out to test for differences between time periods. Analyses were carried out on both the full data set and that of the 82 h station off NSW.

Mean daily food consumption ($C$) was estimated from data for mean stomach fullness per tow obtained at the single station off NSW. The method of Eggers (1977, 1979) was used, because it appears more robust for use with field data than the method of Elliott & Persson (1978), particularly when digestion rate cannot be determined in the laboratory (Boisclair & Leggett 1988):

$$C = 24 \times S \times R \quad (1)$$

where $S$ = mean stomach fullness (g kg$^{-1}$ body weight) over 24 h, and $R$ = digestion rate per hour. $R$ is determined from the apparent rate of food evacuation, based upon diel differences in stomach fullness:

$$S_t = S_0 \, e - R_t \quad (2)$$

where $t$ = time. Using the natural logarithmic transformation of Eq. (2), $R$ was estimated by linear regression analysis.

$$\ln (S_t) = \ln (S_0) - R_t \quad (3)$$

Empty stomachs were omitted from this analysis, because empty stomachs bias estimates of evacuation rate, since the time of emptying is not known (Olson & Mullen 1986). However, our estimate of digestion rate and food consumption will have a conservative bias if the orange roughy do not entirely cease feeding during the period of greatest decline in mean stomach fullness.

## RESULTS

### Diet

A total of 7486 stomachs was examined, 4573 from 1988 and 2913 from 1989. Of this total, 41 % of stomachs (3049) contained food (45 % from 1988 and 34 % from 1989). The diet of orange roughy in south-eastern Australian waters was found to consist of natant decapods, mysids, amphipods, benthopelagic fish and squid (see Tables 2 to 5; Fig. 2). *Acanthephyra pelagica* and an unidentified species of *Pasiphae* were the most common carid prawns found, and *Sergestes* (*Sergestes*) *arcticus* was the predominant penaeid. *Gnathophausia* sp. was the largest mysid identified; smaller mysid specimens were difficult to identify but were probably *Boreomysis* sp. (B. Griffiths, CSIRO, pers. comm.). Two species of amphipods from the family Lyssianassidae were identified: *Eurythenes grillus* and *Trischizostoma nicaeense*. Most fish were unidentifiable, but *Chauliodus sloani* was easily identified even in advanced stages of digestion because the jaws of this species are distinctive and were digested at a slower rate than the rest of the fish. Myctophids were common in orange roughy stomachs but in their half-digested state could not always be identified further. However, *Lampanyctus* spp. and *Lampichthys* spp. were identified and most of the unidentified myctophids were thought to be from these genera. The rapid deterioration of squid made identification impossible, but some beaks from the families Onychoteuthidae, Histioteuthidae, Cranchiidae and Brachioteuthidae were identified.

### Changes in diet with size and depth

The diet shifted from predominantly Crustacea in the smaller orange roughy to fish in the larger animals (Fig. 3). Squid became important in the diet of orange roughy greater than 20 cm, comprising 15 to 20 % of prey weight.

The frequency with which crustaceans and fish were eaten by orange roughy varied significantly with depth (Fig. 4). The effect of depth varied both in the 2 years of the study and with different size groups of orange roughy (Table 1). However, the effect of size became consistent when juveniles and adults were separated for analysis: size was always a significant effect in immature but not in mature size-classes.

Depth-related changes in the diet of mature orange roughy were often inversely related to those of immature fish (Fig. 4). Crustaceans occurred least frequently in the diet of immature orange roughy at a minimum of 900 m in 1988 (Fig. 4a) and at 900 to 1000 m in 1989 (Fig. 4b) but became more frequent in deeper water,

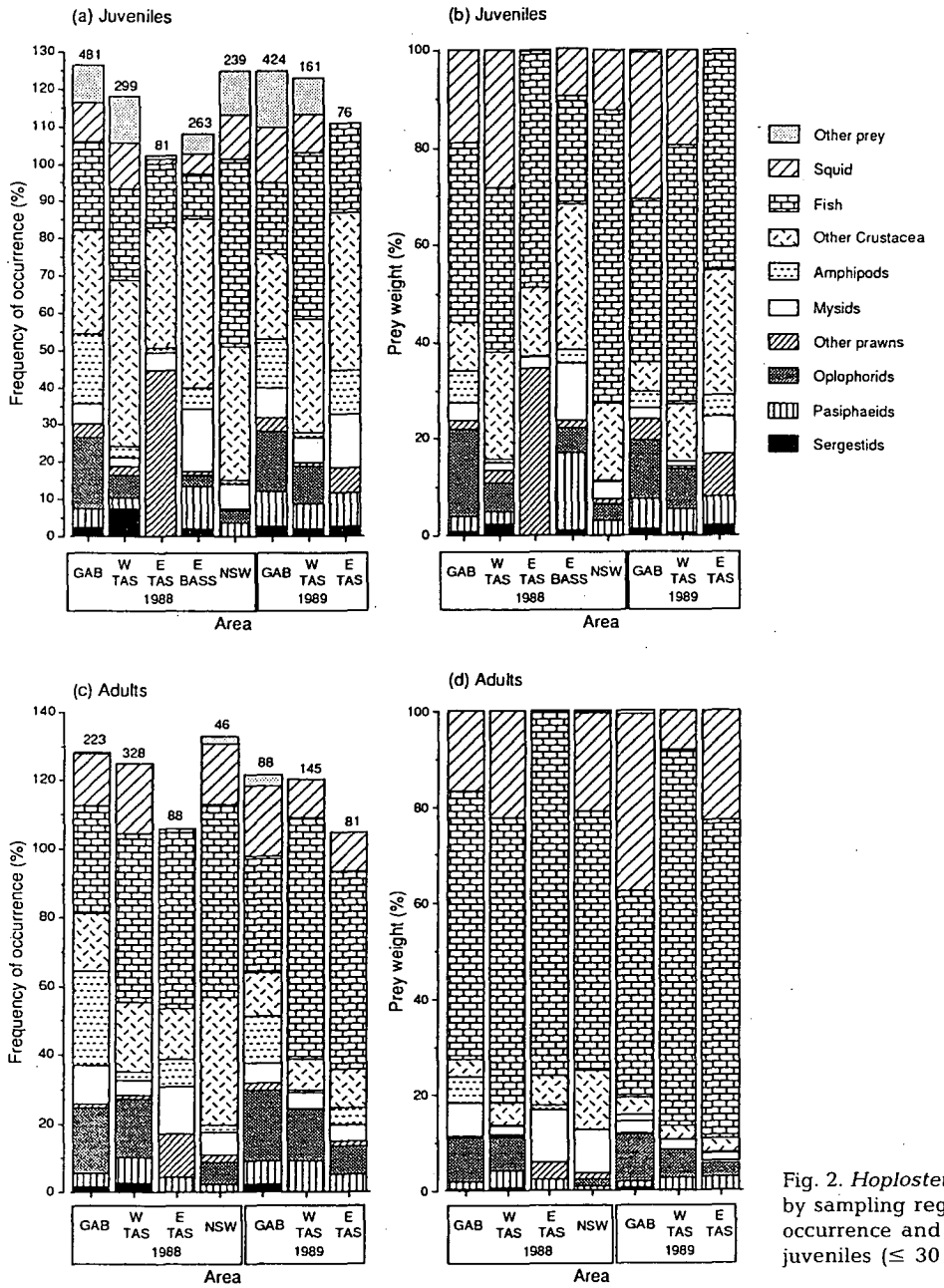


Fig. 2. *Hoplostethus atlanticus*. Dietary composition by sampling region based upon (a, c) frequency of occurrence and (b, d) total prey weight, for (a, b) juveniles (≤ 30 cm SL) and (c, d) adults (> 30 cm SL)

whereas crustaceans in the adult diet peaked at 800 m depth in 1988 and at 900 m in 1989 and then declined in deeper water. In contrast, fish were most frequent in juvenile orange roughy at a depth of 900 m in 1988 (Fig. 4c) and at around 900 to 1000 m in 1989 (Fig. 4d) and then declined in deeper water. Fish were least common in the largest orange roughy (≥ 35 cm) at 900 m but increased significantly in both years at deeper depths (Fig. 4c, d; Table 1). Both mature size-classes fed to a greater extent on fish and less on crustaceans in 1989 [year × depth (adults): Table 1] than in 1988. The frequency with which squid occurred in the diet of orange roughy (Fig. 4e, f) did not vary significantly with depth, but the larger immature fish ate proportionately more squid than the smaller classes.

### Regional and interannual differences in diet

The rank order of prey categories in the diet of orange roughy did not differ significantly throughout the survey area and between years, based upon analysis of frequency of occurrence data [$W$ (adults) = 0.695, $T$ = 58.25, $p < 0.005$; $W$ (juveniles) = 0.859, $T$ = 69.58,

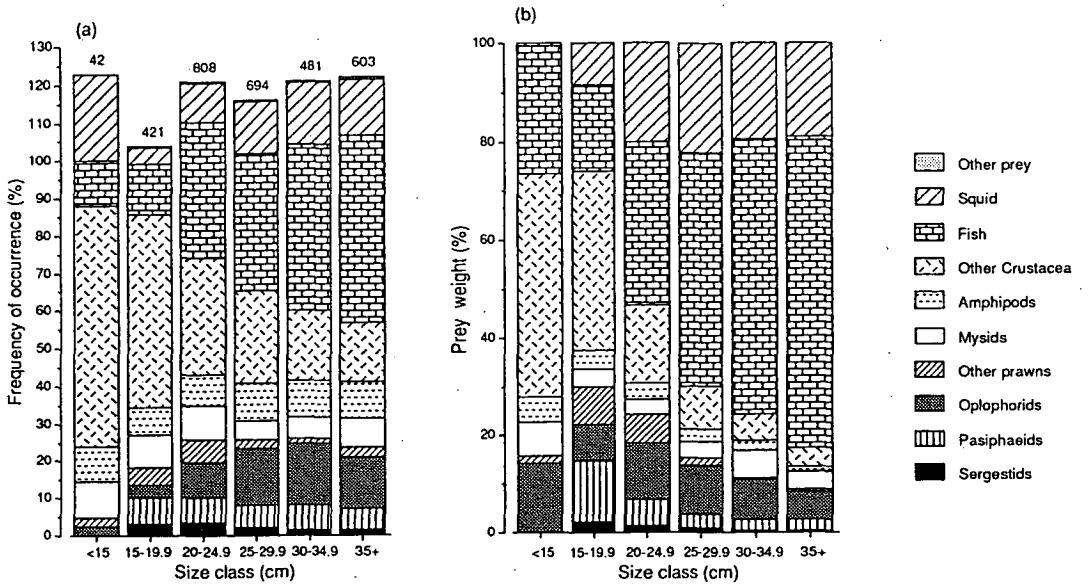


Fig. 3. *Hoplostethus atlanticus*. Dietary composition of size classes by (a) frequency of occurrence and (b) percentage of total prey weight

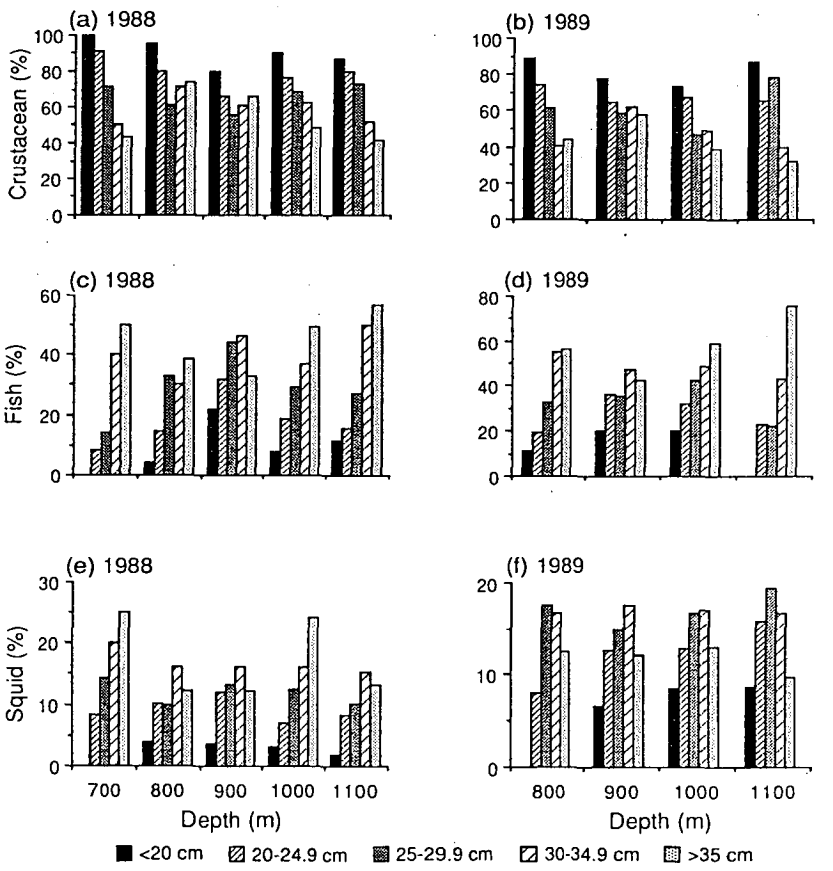


Fig. 4. *Hoplostethus atlanticus*. Proportions of prey in the diet by depth, size, and year: consumption of crustaceans in (a) 1988 and (b) 1989; consumption of fish in (c) 1988 and (d) 1989; consumption of squid in (e) 1988 and (f) 1989

$p < 0.005$] or prey weight [$W$ (adults) = 0.892, $T$ = 64.22, $p < 0.005$; $W$ (juveniles) = 0.713, $T$ = 57.79, $p < 0.005$]. However, there were significant differences in the actual proportions of some prey categories.

### Immature fish

The incidence of feeding in immature fish was significantly higher in 1988 (43.2 %) than in 1989 (35.1 %)

Table 1. *Hoplostethus atlanticus*. Significant chi-squared statistics from 4-way contingency table analyses to determine the relationship between occurrence of prey, depth of capture, size of orange roughy and year

| Prey<br>Effect | All data<br>$\chi^2$, df, p | Juveniles<br>$\chi^2$, df, p | Adults<br>$\chi^2$, df, p |
|---|---|---|---|
| Crustacea | | | |
| Depth × Size | 51.32, 12, *** | | |
| Year × Depth | 10.04, 3, * | 8.03, 3, * | 9.17, 3, * |
| Size | | 69.92, 2, *** | |
| Fish | | | |
| Depth × Size | 54.35, 12, *** | | 12.65, 3, ** |
| Year × Depth | 9.20, 3, * | 8.95, 3, * | |
| Year | | | 11.77, 1, *** |
| Size | | 66.88, 2, *** | |
| Squid | | | |
| Year | | 4.37, 1 * | |
| Size | 45.49, 4, *** | 28.95, 2, *** | |

* $0.01 < p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

(Pearson's $\chi^2_{(1)} = 31.73$, $p < 0.005$); and mean stomach fullness was 79 % higher in 1988 (Tables 2 & 3). Crustaceans constituted a large proportion of their diet: about 50 % by weight in 1988 and 40 % in 1989 (Fig. 2a, b).

Amphipods occurred with variable frequency but were most common in the GAB samples in 1988 (time × area: $\chi^2_{(2)} = 12.24$, $p < 0.005$). Pasiphaeids and mysids were found more frequently in 1989 ($\chi^2_{(1)} = 14.86$, $p < 0.001$ and $\chi^2_{(1)} = 10.34$, $p < 0.005$ respectively) and oplophorids were more frequent in GAB fish (area: $\chi^2_{(2)} = 75.51$, $p < 0.001$). Juveniles in WTas in 1989 ate fish most frequently (time × area: $\chi^2_{(2)} = 21.17$, $p < 0.001$). Juveniles on the east coast of Tasmania did not eat squid, but there were no differences in its consumption in the other 2 areas.

### Adults

The incidence of feeding in mature size-classes was, as in juveniles, higher in 1988 (48.9 %) than in 1989 (32.0 %) (Pearson's $\chi^2_{(1)} = 67.75$, $p < 0.005$), and mean stomach fullness was 61 % higher in 1988 (Tables 4, 5).

Only a few regional differences in diet were significant. Amphipods were twice as common in stomachs in 1988 than in 1989 ($\chi^2_{(1)} = 9.69$, $p < 0.01$) and also occurred in stomachs of fish from the GAB 4 to 10 times more frequently than anywhere else ($\chi^2_{(2)} = 94.16$, $p < 0.01$). Mysids were less frequent on the west coast of Tasmania than in the GAB or east Tasmania ($\chi^2_{(2)} = 10.42$, $p < 0.01$). The occurrence of fish in stomachs varied significantly but exhibited no consistent patterns (time × area: $\chi^2_{(2)} = 6.03$, $p < 0.05$); fish were most frequent in 1989 stomachs in WTas. The occurrence of squid also varied with time and area ($\chi^2_{(2)} = 14.56$, $p < 0.01$), but the greatest proportion of fish eating squid occurred in the GAB in 1989, and the least in ETas.

## Diet within aggregations

An aggregation of orange roughy consisting wholly of adult fish was sampled in the GAB in 1988. The incidence of feeding was significantly higher in the aggregation (69 %) than in adult fish from the rest of the GAB area (52 %) (Pearson's $\chi^2_{(1)} = 8.53$, $p < 0.005$). However, the mean stomach fullness (± SE) of the 3 tows in the aggregation (6.6 ± 1.8 g kg$^{-1}$) was not significantly different (*t*-test, $t_{(48)} = 9.349$) to that of the rest of the GAB tows (5.9 ± 1.3 g kg$^{-1}$). Amphipods occurred significantly more frequently in fish from the aggregation than in 'non-aggregation' fish (Pearson's $\chi^2_{(1)} = 13.46$, $p = 0.002$), but pasiphaeids occurred significantly less often (Fisher's Exact test, $p = 0.003$) (Fig. 5). Fish sampled from a small aggregation off east Tasmania in 1989 were not different from fish from the rest of the region in either incidence of prey or stomach fullness.

## Diel feeding periodicity

### Periodicity in stomach fullness

Data collected at a single site off NSW over 42 h indicated that mean stomach fullness of adult orange roughy peaked in the middle of the night, after which it declined steadily until midday or evening (Fig. 6). Based upon the mean of the rates of decline in stomach fullness measured over each of 3 days, the instantane-

Table 2. *Hoplostethus atlanticus*. Percentage of total prey weight (%W) and frequency of occurrence (%F) of prey items in the diet of juveniles during 1988. See Fig. 1 for abbreviations of sampling areas

| Prey species | GAB | | WTas | | ETas | | EBass | | NSW | | Total | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | %W | %F | %W | %F | %W | %F | %W | %F | %W | %F | %W | %F |
| **Crustacea** | | | | | | | | | | | | |
| Unidentified | 10.3 | 27.9 | 22.2 | 44.8 | 12.1 | 30.9 | 29.7 | 45.2 | 15.9 | 36.0 | 16.0 | 36.5 |
| Copepoda | 0 | 0 | 0 | 0 | 1.9 | 1.2 | 0 | 0 | 0 | 0 | 0.1 | 0.1 |
| Mysidacea | | | | | | | | | | | | |
| Unidentified | 2.2 | 5.0 | 1.7 | 2.3 | 1.8 | 3.7 | 5.1 | 14.4 | 2.3 | 5.4 | 2.3 | 6.2 |
| *Gnathophausia* sp. | 1.2 | 0.2 | 0 | 0 | 0.5 | 1.2 | 6.7 | 2.3 | 1.2 | 1.3 | 1.4 | 0.8 |
| Amphipoda | 6.7 | 18.7 | 0.7 | 3.0 | 0.4 | 1.2 | 3.0 | 5.7 | 0.3 | 0.8 | 3.4 | 8.6 |
| Decapoda | | | | | | | | | | | | |
| Penaidae | | | | | | | | | | | | |
| Unidentified | 0.2 | 0.8 | 0.1 | 0.3 | 11.4 | 6.2 | 0 | 0 | 0 | 0 | 0.7 | 0.7 |
| *Sergestes* (*Sergestes*) *arcticus* | 0.7 | 2.3 | 2.4 | 7.4 | 0 | 0 | 1.1 | 1.9 | 0 | 0 | 1.0 | 2.8 |
| Caridae | | | | | | | | | | | | |
| Unidentified | 1.5 | 3.1 | 2.5 | 2.0 | 23.2 | 38.3 | 1.5 | 1.1 | 1.1 | 0.4 | 2.8 | 4.0 |
| *Pasiphae* spp. | 3.2 | 5.0 | 2.4 | 3.0 | 0 | 0 | 15.8 | 11.4 | 3.2 | 3.8 | 4.0 | 5.3 |
| *Acanthephyra pelagica* | 16.9 | 18.3 | 5.9 | 6.0 | 0 | 0 | 5.2 | 3.0 | 3.3 | 3.3 | 9.8 | 9.0 |
| *Oplophorus novaezelandiae* | 1.2 | 1.0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.5 | 0.4 |
| **Pisces** | | | | | | | | | | | | |
| Unidentified | 26.5 | 20.8 | 24.2 | 21.1 | 19.9 | 6.2 | 17.0 | 10.6 | 50.6 | 45.6 | 29.2 | 22.4 |
| Gonostomatidae | 4.6 | 0.8 | 1.2 | 0.3 | 0 | 0 | 0 | 0 | 0 | 0 | 2.3 | 0.4 |
| Chauliodontidae | | | | | | | | | | | | |
| *Chauliodus sloani* | 1.9 | 0.6 | 0.8 | 0.3 | 0 | 0 | 3.8 | 0.4 | 2.7 | 0.4 | 1.9 | 0.4 |
| Myctophidae | | | | | | | | | | | | |
| Unidentified | 1.7 | 0.8 | 5.8 | 1.7 | 2.2 | 1.2 | 1.4 | 1.1 | 0 | 0 | 3.7 | 1.7 |
| *Lampanyctus* spp. | 1.6 | 0.6 | 1.6 | 0.7 | 0 | 0 | 0 | 0 | 0 | 0 | 1.1 | 0.4 |
| *Lampichthys* sp. | 0 | 0 | 0.2 | 0.3 | 6.7 | 2.5 | 0 | 0 | 7.1 | 4.2 | 0.4 | 0.2 |
| Macrouridae | | | | | | | | | | | | |
| *Coryphaenoides* spp. | 0.3 | 0.2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.1 | 0.1 |
| Apogonidae | | | | | | | | | | | | |
| *Epigonus lenimen* | 0 | 0 | 0 | 0 | 19.9 | 7.4 | 0 | 0 | 0 | 0 | 1.0 | 0.4 |
| **Mollusca** | | | | | | | | | | | | |
| Cephalopoda | 19.2 | 10.2 | 28.3 | 12.4 | 0.1 | 1.2 | 9.8 | 5.3 | 12.3 | 11.7 | 18.3 | 9.5 |
| Total weight of prey (g) | 3359.8 | | 1850.9 | | 406.0 | | 688.6 | | 1443.7 | | 7749.0 | |
| Total stomachs examined | 1140 | | 650 | | 168 | | 673 | | 526 | | 3157 | |
| Stomachs with food present (%) | 481 (42.3) | | 299 (46.0) | | 81 (48.2) | | 263 (39.1) | | 239 (45.4) | | 1363 (43.2) | |
| Mean of average stomach fullness per tow (g $kg^{-1}$) | 5.16 ± 4.73 | | 6.67 ± 6.56 | | 4.07 ± 3.93 | | 2.96 ± 1.83 | | 3.86 ± 2.03 | | 5.02 ± 4.80 | |
| No. of tows | 61 | | 41 | | 12 | | 23 | | 21 | | 158 | |

ous hourly digestion rate ($R$) was estimated to be 0.097 $h^{-1}$ (Fig. 6). There was supporting evidence of diel periodicity in the full data set, although the pattern was not quite significant (Fig. 7a; Kruskal-Wallis test: $\chi^2_{(272)} = 10.68$, $p = 0.056$).

The data for stomach fullness for juveniles at this station were more variable, and no significant pattern was observed for this station or for the whole data set (Fig. 7b).

## Periodicity in digestion stage

Although a significant diel pattern of stomach fullness was not observed in juvenile orange roughy, the juveniles showed significant diel differences in the digestion stage of the stomach contents (Fig. 8) (juveniles: $\chi^2_{(10)} = 30.97$, $p < 0.001$). The highest proportions with food in the early stages of digestion were observed in the afternoon and evening (12:00 to 20:00 h), while the highest proportion of stomachs with food in the later stages of digestion was obtained in the morning (08:00 to 12:00 h). These results are consistent with a pattern of feeding in the afternoon and first half of the night, with little feeding from midnight to midday. However, it should be noted that over 50% of juvenile and adult roughy stomachs were empty at all times, and the highest proportion of stomachs containing food were consistently in the most advanced stage of digestion. The lack of clearer diel patterns in the full data set is not surprising, considering that the depths, areas and time periods of the study were combined for our analysis.

Table 3. *Hoplostethus atlanticus*. Percentage of total prey weight (%W) and frequency of occurrence (%F) of prey items in the diet of juveniles during 1989. See Fig. 1 for abbreviations of sampling areas

| Prey species | GAB | | WTas | | ETas | | EBass | | Total | |
|---|---|---|---|---|---|---|---|---|---|---|
| | %W | %F | %W | %F | %W | %F | %W | %F | %W | %F |
| **Polychaeta** | 0.1 | 0.5 | 0 | 0 | 0 | 0 | 0 | 0 | 0.1 | 0.3 |
| **Crustacea** | | | | | | | | | | |
| Unidentified | 6.2 | 22.9 | 11.7 | 30.4 | 25.7 | 42.1 | 7.3 | 27.8 | 8.7 | 27.0 |
| Mysidacea | | | | | | | | | | |
| Unidentified | 1.4 | 6.8 | 0.9 | 6.8 | 5.2 | 13.2 | 0 | 0 | 1.3 | 7.4 |
| *Gnathophausia* sp. | 1.0 | 1.2 | 0 | 0 | 2.6 | 1.3 | 0 | 0 | 0.8 | 0.9 |
| Amphipoda | 3.3 | 13.0 | 0.1 | 1.2 | 4.3 | 11.8 | 0 | 0 | 2.3 | 9.7 |
| Decapoda | | | | | | | | | | |
| Penaidae | | | | | | | | | | |
| Unidentified | 0 | 0 | 0 | 0 | 4.2 | 1.3 | 0 | 0 | 0.2 | 0.1 |
| *Plesiopenaeus edwardsianus* | 0.8 | 0.2 | 0 | 0 | 0 | 0 | 0 | 0 | 0.5 | 0.1 |
| *Sergestes (Sergestes) arcticus* | 1.4 | 2.6 | 0.4 | 1.9 | 2.1 | 2.6 | 0 | 0 | 1.1 | 2.4 |
| Caridae | | | | | | | | | | |
| Unidentified | 1.3 | 2.1 | 0.6 | 0.6 | 4.7 | 5.3 | 0 | 0 | 1.2 | 2.1 |
| *Pasiphae* spp. | 6.1 | 9.4 | 5.1 | 6.8 | 5.8 | 9.2 | 0.6 | 5.6 | 5.6 | 8.7 |
| *Acanthephyra pelagica* | 10.5 | 13.9 | 3.5 | 4.3 | 0 | 0 | 0 | 0 | 7.6 | 9.7 |
| *A. quadrispinosa* | 0.9 | 1.7 | 4.6 | 5.6 | 0 | 0 | 0 | 0 | 1.9 | 2.4 |
| *Oplophorus novaezelandiae* | 0.7 | 0.5 | 0 | 0 | 0 | 0 | 0 | 0 | 0.5 | 0.3 |
| *Plesionika martia* | 0.4 | 0.2 | 0 | 0 | 0 | 0 | 0 | 0 | 0.3 | 0.1 |
| *Lipkius holthuisi* | 1.7 | 0.9 | 0.1 | 0.6 | 0 | 0 | 0 | 0 | 1.1 | 0.7 |
| *Nematocarcinus sigmoideus* | 0.2 | 0.2 | 0 | 0 | 0 | 0 | 0 | 0 | 0.1 | 0.1 |
| **Pisces** | | | | | | | | | | |
| Unidentified | 17.8 | 14.4 | 40.7 | 35.4 | 26.1 | 19.7 | 48.4 | 38.9 | 25.8 | 20.6 |
| Gonostomatidae | 3.6 | 0.7 | 1.7 | 1.9 | 0 | 0 | 0 | 0 | 2.7 | 0.9 |
| Neoscopelidae | | | | | | | | | | |
| *Neoscopelus* sp. | 1.0 | 0.2 | 0 | 0 | 0 | 0 | 0 | 0 | 0.7 | 0.1 |
| Chauliodontidae | | | | | | | | | | |
| *Chauliodus sloani* | 3.9 | 0.9 | 1.8 | 1.2 | 0 | 0 | 0 | 0 | 3.0 | 0.9 |
| Myctophidae | | | | | | | | | | |
| Unidentified | 0 | 0 | 1.0 | 1.9 | 0 | 0 | 0 | 0 | 0.3 | 0.4 |
| *Lampanyctus* spp. | 0.1 | 0.2 | 3.5 | 1.9 | 19.3 | 3.9 | 10.3 | 5.6 | 2.4 | 1.2 |
| Bathylagidae | 1.3 | 0.5 | 1.1 | 0.6 | 0 | 0 | 0 | 0 | 1.1 | 0.4 |
| Macrouridae | | | | | | | | | | |
| *Coryphaenoides* spp. | 0 | 0 | 2.9 | 0.6 | 0 | 0 | 0 | 0 | 0.8 | 0.1 |
| Other fish | 5.8 | 2.1 | 0.7 | 1.2 | 0 | 0 | 0 | 0 | 3.8 | 1.6 |
| **Mollusca** | | | | | | | | | | |
| Cephalopoda | 30.3 | 14.9 | 19.5 | 9.9 | 0 | 0 | 33.4 | 27.8 | 25.9 | 12.4 |
| **Tunicata** | | | | | | | | | | |
| *Pyrosoma* sp. | 0.4 | 0.9 | 0 | 0 | 0 | 0 | 0 | 0 | 0.3 | 0.6 |
| Total weight of prey | 2508.7 | | 1100.8 | | 191.3 | | 155.5 | | 3956.3 | |
| Total stomachs examined | 1050 | | 642 | | 181 | | 56 | | 1929 | |
| Stomachs with food present (%) | 424 (40.4) | | 1641 (25.0) | | 76 (42.0) | | 18 (32.1) | | 679 (35.1) | |
| Mean of average stomach fullness per tow (g $kg^{-1}$) | 5.24 ± 5.78 | | 3.61 ± 3.61 | | 2.16 ± 1.72 | | 6.99 ± 2.72 | | 2.81 ± 2.47 | |
| No. of tows | 78 | | 63 | | 19 | | 3 | | 163 | |

### Food consumption

Based upon our estimate of $R$ and the mean stomach fullness (4.94 g $kg^{-1}$ for adults; Tables 4, 5), orange roughy were estimated to consume 11.50 g $kg^{-1}$ (= 1.15 % body wt) over the 24 h day. The digestion rate of juveniles was not estimated separately. However, their mean stomach fullness was similar to that of the adults (3.90 g $kg^{-1}$ body wt) (Tables 2, 3), and if the same digestion rate is assumed, their daily food consumption may be estimated to be 9.08 g $kg^{-1}$ (= 0.91 % body wt).

## DISCUSSION

The results of our dietary analyses of Australian *Hoplostethus atlanticus* are consistent with those obtained elsewhere in the species' geographical range. *H. atlanticus* feeds on bentho- and mesopelagic crus-

Table 4. *Hoplostethus atlanticus*. Percentage of total prey weight (% W) and frequency of occurrence (% F) of prey items in the diet of adults during 1988. See Fig. 1 for abbreviations of sampling areas

| Prey species | GAB | | WTas | | ETas | | EBass | | NSW | | Total | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | %W | %F | %W | %F | %W | %F | %W | %F | %W | %F | %W | %F |
| **Polychaeta** | <0.1 | 0.4 | 0 | 0 | 0 | 0 | 0 | 0 | 0.5 | 2.2 | <0.1 | 0.3 |
| **Crustacea** | | | | | | | | | | | | |
| Unidentified | 3.5 | 16.1 | 4.6 | 20.1 | 3.5 | 12.5 | 2.9 | 28.6 | 12.4 | 37.0 | 4.7 | 19.2 |
| Copepoda | 0.1 | 0.9 | 0 | 0 | 2.8 | 2.3 | 0 | 0 | 0 | 0 | 0.3 | 0.6 |
| Mysidacea | | | | | | | | | | | | |
| Unidentified | 2.0 | 9.4 | 0.9 | 3.4 | 3.6 | 6.8 | 0 | 0 | 1.3 | 2.2 | 1.5 | 5.6 |
| *Gnathophausia* sp. | 4.9 | 1.8 | 1.2 | 0.9 | 7.4 | 6.8 | 40.1 | 28.6 | 7.6 | 4.3 | 4.2 | 2.5 |
| Amphipoda | 5.4 | 27.4 | 0.3 | 2.7 | 0.9 | 8.0 | 0 | 0 | 0.1 | 2.2 | 1.8 | 11.3 |
| Decapoda | | | | | | | | | | | | |
| Penaidae | | | | | | | | | | | | |
| Unidentified | 0 | 0 | 0.1 | 0.6 | 2.2 | 5.7 | 0 | 0 | 0 | 0 | 0.3 | 1.0 |
| *Sergestes* (*Sergestes*) *arcticus* | 0.2 | 1.3 | 0.4 | 2.7 | 0 | 0 | 0 | 0 | 0 | 0 | 0.3 | 1.7 |
| Caridae | | | | | | | | | | | | |
| Unidentified | 0.2 | 0.9 | 0.2 | 0.3 | 1.1 | 5.7 | 5.0 | 14.3 | 1.4 | 2.2 | 0.3 | 1.3 |
| *Pasiphae* sp. | 1.5 | 4.0 | 3.6 | 7.3 | 2.3 | 4.5 | 0 | 0 | 0.9 | 2.2 | 2.7 | 5.5 |
| *Acanthephyra pelagica* | 7.9 | 16.6 | 6.7 | 16.5 | 0 | 0 | 3.2 | 14.3 | 1.4 | 6.5 | 6.0 | 13.7 |
| *A. quadrispinosa* | 0.1 | 0.4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | <0.1 | 0.1 |
| *Oplophorus novaezelandiae* | 1.3 | 2.2 | 0.3 | 0.9 | 0 | 0 | 0 | 0 | 0 | 0 | 0.5 | 1.2 |
| *Pontophilus* sp. | 0 | 0 | 0 | 0 | 0.3 | 1.1 | 0 | 0 | 0 | 0 | <0.1 | 0.1 |
| **Pisces** | | | | | | | | | | | | |
| Gonostomatidae | 7.0 | 2.2 | 1.3 | 0.6 | 2.0 | 1.1 | 0 | 0 | 0 | 0 | 2.9 | 1.2 |
| Unidentified | 21.7 | 18.4 | 44.8 | 40.9 | 22.6 | 23.9 | 48.8 | 42.9 | 50.8 | 50.0 | 36.3 | 32.1 |
| Chauliodontidae | | | | | | | | | | | | |
| *Chauliodus sloani* | 24.1 | 8.5 | 5.2 | 1.5 | 10.2 | 3.4 | 0 | 0 | 0 | 0 | 10.9 | 3.9 |
| Myctophidae | | | | | | | | | | | | |
| Unidentified | 2.6 | 1.8 | 4.0 | 4.3 | 8.6 | 5.7 | 0 | 0 | 2.9 | 6.5 | 3.8 | 3.8 |
| *Gymnoscopelus* sp. | 0 | 0 | 0 | 0 | 3.4 | 2.3 | 0 | 0 | 0 | 0 | 0.3 | 0.3 |
| *Lampanyctus* spp. | 0.6 | 0.9 | 0.2 | 0.3 | 0 | 0 | 0 | 0 | 0 | 0 | 0.3 | 0.4 |
| *Lampichthys* sp. | 0 | 0 | 1.1 | 0.6 | 3.0 | 3.4 | 0 | 0 | 0 | 0 | 0.9 | 0.7 |
| Paralepididae | | | | | | | | | | | | |
| *Lestidiops pacifica* | 0 | 0 | 0.9 | 0.3 | 0 | 0 | 0 | 0 | 0 | 0 | 0.5 | 0.1 |
| Macrouridae | | | | | | | | | | | | |
| *Lepidorhynchus denticulatus* | 0 | 0 | 0 | 0 | 6.9 | 1.1 | 0 | 0 | 0 | 0 | 0.7 | 0.1 |
| *Coryphaenoides* spp. | 0 | 0 | 1.9 | 0.9 | 8.0 | 2.3 | 0 | 0 | 0 | 0 | 1.8 | 0.7 |
| Apogonidae | | | | | | | | | | | | |
| *Epigonus lenimen* | 0 | 0 | 0 | 0 | 11.1 | 8.0 | 0 | 0 | 0 | 0 | 1.1 | 1.0 |
| **Mollusca** | | | | | | | | | | | | |
| Cephalopoda | 16.9 | 15.2 | 22.2 | 20.7 | 0.1 | 1.1 | 0 | 0 | 20.7 | 17.4 | 17.9 | 16.0 |
| Total weight of prey (g) | 3092.1 | | 5530.3 | | 1001.6 | | 240.8 | | 590.2 | | 10455.0 | |
| Total stomachs examined | 401 | | 649 | | 263 | | 16 | | 87 | | 1416 | |
| Stomachs with food present (%) | 223 (55.6) | | 328 (50.5) | | 88 (33.5) | | 7 (43.8) | | 46 (52.9) | | 692 (48.9) | |
| Mean of average stomach fullness per tow (g $kg^{-1}$) | 5.56 ± 8.89 | | 6.53 ± 6.45 | | 2.73 ± 1.97 | | 11.13 ± 14.35 | | 4.55 ± 3.16 | | 6.16 ± 8.10 | |
| No. of tows | 50 | | 40 | | 13 | | 12 | | 14 | | 129 | |

tacea, fish and squid. Pasiphaeids, oplophorids and sergestids were the major decapod taxa consumed, as in New Zealand (Rosecchi et al. 1988). Kotlyar & Lipskaya (1980) found pasiphaeids to be important in the diet of fish off the West Australian and Madagascar Ridges. The main families of the fish eaten by *H. atlanticus* were the chauliodontids and myctophids, as in the New Zealand study (Rosecchi et al. 1988). Squid comprised about 10 % of the diet in terms of frequency of occurrence, which is consistent with previous reports (Kotlyar & Lipskaya 1980, Rosecchi et al. 1988).

The diet of the orange roughy in the 3 areas and between the 2 years was broadly similar in terms of the overall ranking of prey groups. However, there were some significant differences in the incidence of particular prey groups in the diet among areas or between years. The dietary data suggest orange roughy are opportunistic feeders, so the variability in the data may

Table 5. *Hoplostethus atlanticus*. Percentage of total prey weight (% W) and frequency of occurrence (% F) of prey items in the diet of adults during 1989. See Fig. 1 for abbreviations of sampling areas

| Prey species | GAB | | WTas | | ETas | | EBass | | Total | |
|---|---|---|---|---|---|---|---|---|---|---|
| | %W | %F | %W | %F | %W | %F | %W | %F | %W | %F |
| **Crustacea** | | | | | | | | | | |
| Unidentified | 3.8 | 12.5 | 2.8 | 9.0 | 2.8 | 11.1 | 0 | 0 | 3.0 | 10.5 |
| Mysidacea | | | | | | | | | | |
| Unidentified | 0.4 | 3.4 | 0.1 | 2.8 | 0.1 | 1.2 | 0 | 0 | 0.2 | 2.5 |
| *Gnathophausia* sp. | 2.1 | 2.3 | 2.1 | 2.1 | 1.5 | 3.7 | 0 | 0 | 1.9 | 2.5 |
| Amphipoda | 1.2 | 13.6 | <0.1 | 0.7 | 0.3 | 4.9 | 0 | 0 | 0.4 | 5.4 |
| Decapoda | | | | | | | | | | |
| Penaidae | | | | | | | | | | |
| *Sergestes* (*Sergestes*) *arcticus* | 0.5 | 2.3 | 0 | 0 | 0 | 0 | 0 | 0 | 0.1 | 0.6 |
| Caridae | | | | | | | | | | |
| Unidentified | 0.3 | 2.3 | 0 | 0 | 0.4 | 1.2 | 0 | 0 | 0.2 | 1.0 |
| *Pasiphae* spp. | 1.4 | 6.8 | 2.6 | 89.0 | 2.8 | 4.9 | 0 | 0 | 2.4 | 7.3 |
| *Acanthephyra pelagica* | 2.7 | 10.2 | 1.9 | 4.8 | 0 | 0 | 0 | 0 | 1.6 | 5.1 |
| *A. quadrispinosa* | 3.0 | 10.2 | 3.9 | 10.3 | 0.3 | 1.2 | 0 | 0 | 2.6 | 7.9 |
| *Oplophorus novaezelandiae* | 3.9 | 1.1 | 0 | 0 | 2.6 | 7.4 | 0 | 0 | 1.7 | 2.2 |
| **Pisces** | | | | | | | | | | |
| Unidentified | 11.7 | 22.7 | 51.6 | 56.6 | 48.0 | 49.4 | 0 | 0 | 41.0 | 45.4 |
| Gonostomatidae | 2.1 | 1.1 | 0 | 0 | 0 | 0 | 0 | 0 | 0.5 | 0.3 |
| Scopelasauridae | | | | | | | | | | |
| *Scopelosaurus* sp. | 2.2 | 1.1 | 0 | 0 | 0 | 0 | 0 | 0 | 0.5 | 0.3 |
| Chauliodontidae | | | | | | | | | | |
| *Chauliodus sloani* | 10.2 | 3.4 | 2.0 | 0.7 | 7.0 | 3.7 | 0 | 0 | 5.4 | 2.2 |
| Myctophidae | | | | | | | | | | |
| Unidentified | 0 | 0 | 3.6 | 3.4 | 3.5 | 1.2 | 0 | 0 | 2.7 | 1.9 |
| *Lampanyctus* spp. | 0.7 | 1.1 | 3.9 | 4.1 | 0 | 0 | 0 | 0 | 2.0 | 2.2 |
| Bathylagidae | 0 | 0 | 8.0 | 1.4 | 0 | 0 | 0 | 0 | 3.7 | 0.6 |
| Macrouridae | | | | | | | | | | |
| *Coryphaenoides* spp. | 0 | 0 | 2.5 | 2.1 | 2.1 | 2.5 | 0 | 0 | 1.7 | 1.6 |
| Other fish | 16.3 | 4.5 | 6.7 | 2.1 | 5.6 | 1.2 | 0 | 0 | 8.7 | 2.5 |
| **Mollusca** | | | | | | | | | | |
| Cephalopoda | 36.8 | 20.5 | 8.3 | 11.0 | 23.0 | 11.1 | 100 | 100 | 19.4 | 13.7 |
| **Tunicata** | | | | | | | | | | |
| *Pyrosoma* sp. | 0.7 | 3.4 | 0 | 0 | 0 | 0 | 0 | 0 | 0.2 | 1.0 |
| Total weight of prey | 1280.9 | | 2387.1 | | 1439.9 | | 41.0 | | 5148.9 | |
| Total stomachs examined | 248 | | 483 | | 249 | | 4 | | 984 | |
| Stomachs with food present (%) | 88 (35.5) | | 145 (30.0) | | 81 (32.5) | | 1 (25) | | 315 (32.0) | |
| Mean of average stomach fullness per tow (g $kg^{-1}$) | 4.10 ± 9.89 | | 3.47 ± 3.63 | | 3.82 ± 3.45 | | 6.86 ± 9.70 | | 3.83 ± 7.00 | |
| No. of tows | 61 | | 60 | | 20 | | 2 | | 143 | |

reflect spatial and temporal variation in the abundance of prey species.

As *Hoplostethus atlanticus* grows, fish become increasingly important in its diet, as Kotlyar & Lipskaya (1980) and Rosecchi et al. (1988) reported. Similar shifts in the diet have been observed in other benthopelagic predators, such as *Cyttus traversi* and *Helicolenus percoides* (Blaber & Bulman 1987), as well as in other fishes that are predominantly piscivorous as adults (e.g. Atlantic cod; Daan 1973). On the other hand, 3 benthopelagic macrourid species in Tasmanian waters (*Coelorinchus* spp. 2 and 4 and *Lepidorhynchus denticulatus*) do not exhibit this ontogenetic shift in dietary composition (Blaber & Bulman 1987).

Squid appeared first in the diet of fish over 15 cm. The proportion in the diet was at about the same level throughout the larger size classes. Squid was observed in the diet of orange roughy in the northeast Atlantic and off New Zealand in fish over 20 cm (Mauchline & Gordon 1984, Rosecchi et al. 1988). The importance of squid in terms of proportion of the diet by weight is likely to be under-estimated since it is digested at a greater rate than fish or crustaceans. Often only the squid beaks remained in a stomach.

Resource-partitioning between adult and juvenile orange roughy is suggested by the observed inverse patterns of prey selection. Resource-partitioning among size classes of deepwater fish may be a mechan-

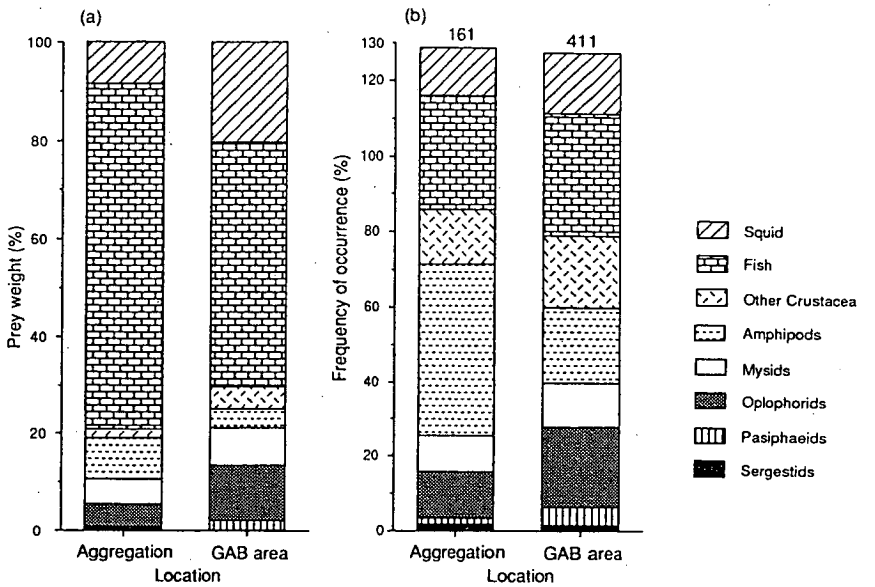


Fig. 5. *Hoplostethus atlanticus*. Comparison of the diet of fish from an aggregation in the Great Australian Bight in 1988 and fish from the Bight area excluding the aggregation sites, by (a) prey weight and (b) frequency of occurrence of adults (< 30 cm SL)

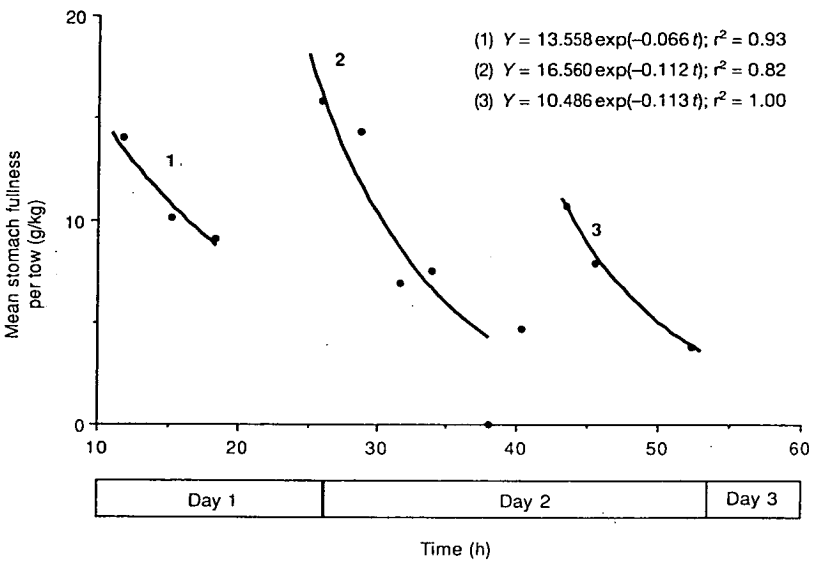


Fig. 6. *Hoplostethus atlanticus*. Mean stomach fullness per tow (g $kg^{-1}$ body weight) of adults at the NSW sampling site over a 42 h period. Regressions were calculated for 3 consecutive periods when stomach fullness declined

ism to reduce intra-specific competition at depths where prey are not abundant (Baird & Hopkins 1981). Such a mechanism might be effective for a species such as *Hoplostethus atlanticus* which is the dominant component of the fish biomass at these depths in the region (Bulman et al. in press). However, hypotheses on competitive interactions are difficult to test with field survey data.

Diel feeding periodicity has not been previously reported for orange roughy (Rosecchi et al. 1988). It may have become apparent in our study due to our 10-fold larger sample size and concentrated sampling at a single site. Diel feeding periodicity is commonly reported for upper slope fishes that make diurnal feeding migrations (e.g. Kinzer & Shulz 1985, Young & Blaber 1986), but non-migratory slope fishes generally do not exhibit diel variation in feeding (Merrett & Roe 1974, Macpherson 1981, Blaber & Bulman 1987). There is no evidence that orange roughy migrates diurnally, but many of its prey apparently do, e.g. *Chauliodus sloani* (Morrow 1964), several species of *Lampanyctus* (Smith & Heemstra 1986) and *Acanthephyra pelagica* and *Sergestes* (*Sergestes*) *arcticus* (Roe 1984). Orange roughy's crepuscular feeding pattern suggests that it is benefitting from migrators rising from mid-slope depths. Diel feeding periodicity was reported in the mesopelagic *Valenciennellus tripunctulatus*, which also does not itself migrate but feeds upon migrators

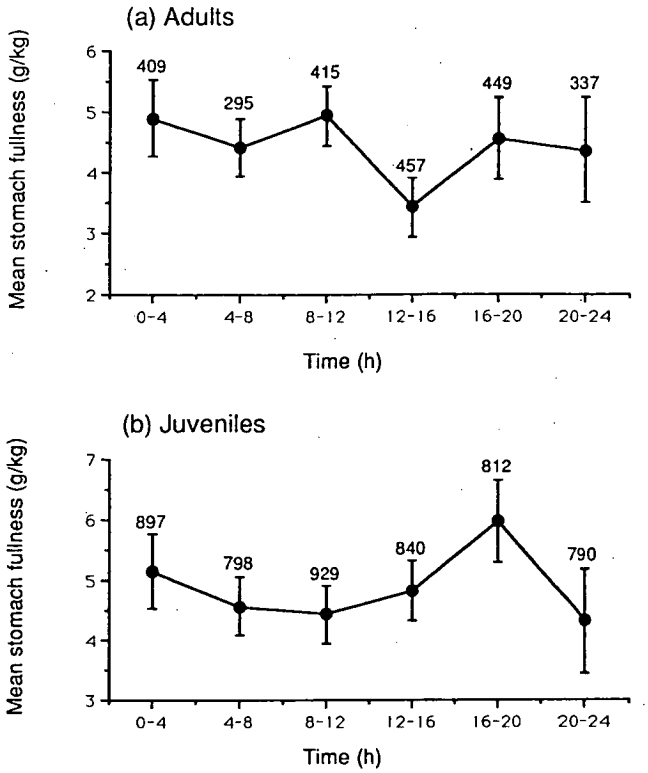


Fig. 7. *Hoplostethus atlanticus*. Mean stomach fullness per tow (g $kg^{-1}$ body weight) over 4 h intervals for (a) adults (> 30 cm SL) and (b) juveniles (≤ 30 cm SL). Total numbers of fish for each time interval are above the standard error bars

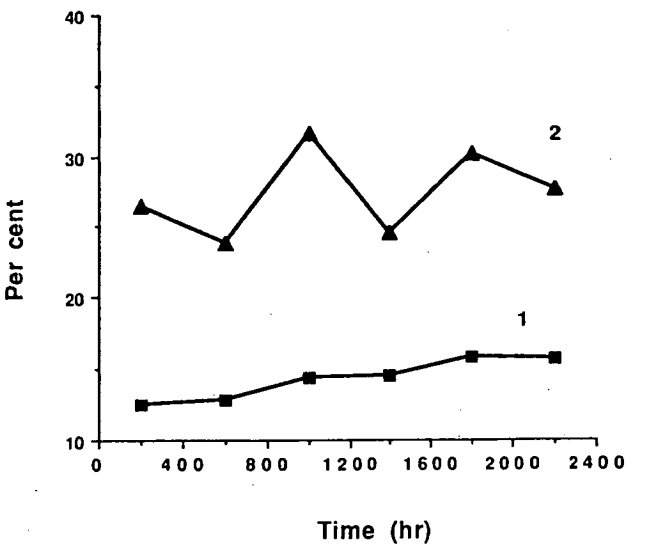


Fig. 8. *Hoplostethus atlanticus*. Proportion of juveniles (≤ 30 cm SL) at early (stage 1) or advanced (stage 2) of digestion at 4 h intervals

that are available only during the day (Merret & Roe 1974).

The high incidence of orange roughy with empty stomachs (> 50 %) fits a general pattern noted for deepwater predator feeding on large invertebrates and fish (Legand & Rivaton 1969, Merrett & Roe 1974). These authors have speculated that this pattern indicates infrequent feeding or rapid digestion rates. The evacuation rate of benthopelagic predators has not been directly measured, but our estimate of gut residence time (< 1 d) suggests that the rate of digestion is comparable to that of other cold-water piscivorous fishes (e.g. Atlantic cod; Jones 1978), but that feeding is infrequent. We found no evidence that orange roughy regurgitate their stomach contents. Orange roughy have an oil-filled swim bladder that is unaffected by pressure changes, which often cause an air-filled swim bladder to force out the stomach contents.

Our estimate of orange roughy food consumption (0.91 and 1.15 % body weight $d^{-1}$ for juveniles and adults, respectively) is closer to estimates of the food consumption of several mesopelagic migrators (0.87 % $d^{-1}$), which are relatively active fishes, than to estimates for bathypelagic non-migrators (0.68 %) (Childress et al. 1980). This result was not expected, since these bathypelagic non-migrators are generally small (15 to 29 cm), short-lived (4 to 8 yr) animals that exhibit rapid growth rates (Torres et al. 1979, Childress et al. 1980). Orange roughy, on the other hand, grows exceptionally slowly, maturing at ~ 20 yr at ~ 30 cm, and achieves a standard length of 45 to 50 cm at 50 to 100 + yr (Mace et al. 1990, Fenton et al. 1991). The relatively high rate of food consumption and low growth rate of orange roughy have clear implications for estimates of the species' metabolism and growth efficiency.

There are no direct measurements of the metabolic rate of orange roughy, but metabolism can be estimated from data on their food consumption, growth, and reproduction, using the mass balance equation

$$aR = G + T \quad (4)$$

where $a$ is the coefficient of assimilation (which we assume equal to 0.8), $R$ is ration, $G$ represents growth and reproduction, and $T$ is metabolism. Available data indicate that the mean growth of orange roughy juveniles (10 to 20 yr old) is 11 % $yr^{-1}$ and of adults (20 to 50 yr) is 2.8 % $yr^{-1}$ (Evans & Wilson 1987, Mace et al. 1990). Annual reproductive effort of orange roughy is ~ 10 % of body weight (Pankhurst & Conrey 1987), so $G$ for adult roughy is ca 15 % $yr^{-1}$ assuming that the energetic content of gonadal tissue is 1.2 that of somatic tissue (Ware 1980). Using our values for daily food consumption ($R$), daily metabolism may be estimated to be 0.70 % body weight for juveniles and 0.88 % for adults. This translates to estimates of oxygen consumption for juveniles of 0.11 l $O_2$ $kg^{-1}$ wet wt $h^{-1}$ and for adults of 0.14, assuming conversions of 1750 kcal $kg^{-1}$ wet wt, which is typical of mesopelagic fishes with a

similar body composition to that of orange roughy (Table 6), and 4.63 kcal $l^{-1}$ $O_2$ (Brett & Groves 1979).

Based upon this exercise, metabolism of orange roughy is comparable to that of mesopelagic migratory species and approximately an order of magnitude higher than that of the bathypelagic non-migrators studied by Torres et al. (1979) (~ 0.01 l $O_2$ $kg^{-1}$ wet wt $h^{-1}$) (Table 6). Torres et al. (1979) apparently measured resting metabolic rates, whereas our estimates are of total field metabolism, so their values should be approximately doubled for comparison. [The *in situ* measurements of Smith & Laver (1981) indicate that the active metabolism of bathypelagic non-migrators may be substantially higher than their resting metabolism (Table 6).] However, the apparent metabolism of orange roughy, which is a member of the mid-slope benthopelagic fauna *sensu* Marshall & Merrett (1977), remains closer to that of mesopelagic migrators than of bathypelagic non-migrators. This is reasonable considering the ecology and composition of orange roughy. The proximate composition of fish is closely related to their metabolism (Torres et al. 1979). Orange roughy does not have the high water and reduced protein, lipid, and ash content that is typical of low-energy bathypelagic non-migrators (Table 6). Many bathypelagic species are not very active, whereas orange roughy may aggregate in areas of high near-bottom currents (~ 25 cm $s^{-1}$; V. Lyne, CSIRO, pers. comm.), and photographs indicate that they maintain a position oriented into the current (unpubl. data).

Related to their apparently high metabolism, the life history of orange roughy differs markedly from that of bathypelagic fishes. Bathypelagic non-migratory fishes typically have high rates of growth and growth efficiency, and non-asymptotic growth, apparently because they conserve energy through lower metabolism and reduced body structure and caloric content (Childress et al. 1980, Mauchline 1988). In contrast, growth in orange roughy is exceptionally slow, highly asymptotic, and very inefficient (about 4 %), apparently related to its relatively high metabolic costs (Table 6). Orange roughy is widely distributed in temperate midslope habitats of the southern oceans and North Atlantic, but is ecologically dominant in areas off Australia and New Zealand. Its dominance, which has led to the development of substantial fisheries, may be limited to regions of high currents and, we speculate, high energy input that can support its metabolic requirements. Clearly, the metabolic and gut evacuation rates of orange roughy should be measured directly, if possible, to test some of the assumptions underlying our preliminary energetic calculations for orange roughy. The biological oceanography of deep-water regions supporting this fish has yet to be characterized.

Table 6. Estimates of food consumption ($R$), metabolism ($T$), growth and reproduction ($G$), gross production efficiency (K = $G/R$), and bodily composition of orange roughy, mesopelagic migrators and bathypelagic non-migrators. SL: standard length; BW: body weight

| | *Hoplostethus atlanticus* | | Mesopelagic migrators | | | | Bathypelagic non-migrators | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Juveniles | Adults | *Stenobrachius leucopsaurus*[a] | *Leuroglossus stilbius*[a] | *Lampanyctus ritteri*[a] | *Lampanyctus alatus* (40–44 mm)[b] | *Borostomias panamensis*[a] | *Lampanyctus regalis*[a] | *Bajacalifornia burragei*[a] | *Cyclothone acclinidens*[f] |
| Minimum depth (m) | 750 | 750 | Surface | Surface | 75 | 40[d] | 500 | 500 | 1000 | 300 |
| Maximum SL (cm) | 30 | >50 | 8.6 | 11.8 | 11.8 | 6.1[d] | 29 | 19.8 | 19.8 | 5.1 |
| % Water | | 67[c] | 67 | 81 | 71 | | 82 | 86 | 86 | 77 |
| % Lipid | | 18 | 13 | 6 | 12 | | 6 | 2 | | 6 |
| % Protein | | 12 | 11 | 7 | 12 | | 4 | 6 | | |
| % Ash | | | 2 | 1 | 2 | | <1 | 1 | | |
| Energy density (kcal $g^{-1}$ wet wt) | | 3 | 1.82 | 1.00 | 1.76 | | 0.70 | 0.60 | 0.57 | 0.37 |
| R (% BW $d^{-1}$) | 0.91 | 1.15 | 0.87 | 0.87 | 0.87 | 2.3 | 0.68 | 0.68 | 0.68 | |
| T (l $O_2$ $kg^{-1}$ BW $h^{-1}$) | 0.11 | 0.14 | 0.07 | 0.024 | 0.059 | | 0.017 | 0.011 | 0.005 | 0.024 (0.10)[f] |
| G (% BW $yr^{-1}$) | 11 | 15 | 93[e] | 138[e] | 102[e] | | 116[e] | 140[e] | 105[e] | |
| K (%) | 3.3 | 3.6 | 15 | 23 | 26 | | 38 | 52 | 68 | |

[a] Data from Childress & Nygaard (1973) and Childress et al. (1980); [b] data from Hopkins & Baird (1985); [c] body composition from Vlieg (1983); [d] data from Smith & Heemstra (1986); [e] does not include reproduction; [f] data from Smith & Laaver (1981) (respiration values are for resting and, in parentheses, active metabolism

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## LITERATURE CITED

Baird, R. C., Hopkins, T. L. (1981). Trophodynamics of the fish *Valenciennellus tripunctulatus*. III. Energetics, resources and feeding strategy. Mar. Ecol. Prog. Ser. 5: 21–28

Blaber, S. J. M., Bulman, C. M. (1987). Diets of fishes of the upper continental slope of eastern Tasmania: content, calorific values, dietary overlap and trophic relationships. Mar. Biol. 95: 345–356

Boisclair, D., Leggett, W. C. (1988). An in situ experimental evaluation of the Elliot and Persson and the Eggers models for estimating fish daily ration. Can. J. Fish. Aquat. Sci. 45: 138–145

Brett, J. R., Groves, T. D. D. (1979). Physiological energetics. In: Hoar, W. S., Randall, D. J. (eds.) Fish physiology, Vol. 8. Academic Press, New York, p. 279–351

Bulman, C. M., Wayte, S. E., Elliott, N. G. (in press). The 1988 and 1989 orange roughy surveys: abundance indices. CSIRO Mar. Lab. Rep. 215

Childress, J. J., Nygaard, M. (1973). The chemical composition of midwater fishes as a function of depth of occurrence off Southern California. Deep Sea Res. 20: 1093–1109

Childress, J. J., Taylor, S. M., Cailliet, G. M., Price, M. H. (1980). Patterns of growth, energy utilization and reproduction in some meso- and bathypelagic fishes off Southern California. Mar. Biol. 61: 27–40

Clarke, T. A. (1978). Diel feeding patterns of 16 species of mesopelagic fishes from Hawaiian waters. Fish. Bull. U.S. 76: 495–513

Conover, W. J. (1971). Practical nonparametric statistics. John Wiley & Sons, New York

Daan, N. (1973). A quantitative analysis of the food intake of the North Sea cod, *Gadus morhua*. Neth. J. Sea Res. 6: 479–517

Eggers, D. M. (1977). Factors in interpreting data obtained by diel sampling of fish stomachs. J. Fish. Res. Bd Can. 34: 290–294

Eggers, D. M. (1979). Comment on some recent methods for estimating food consumption by fish. J. Fish. Res. Bd Can. 36: 1018–1019

Elliot, J. M., Persson, L. (1978). The estimation of daily rates of food consumption for fish. J. Anim. Ecol. 47: 977–991

Evans, K., Wilson, M. A. (1987). A summary of orange roughy biological information: 1981–1985. Dept. of Sea Fisheries, Hobart, Tasmania

Fenton, G. E., Short, S. A., Ritz, D. A. (1991). Age determination of orange roughy, *Hoplostethus atlanticus* (Pisces: Trachichthyidae), using 210 Pb/226 Ra disequilibria. Mar. Biol. 109: 197–202

Gordon, J. D. M., Duncan, J. A. R. (1987). Aspects of the biology of *Hoplostethus atlanticus* and *H. mediterraneus* (Pisces: Berycomorphi) from the slopes of the Rockall Trough and the Porcupine Sea Bight (north-eastern Atlantic). J. mar. biol. Ass. U.K. 67: 119–133

Hopkins, T. L., Baird, R. C. (1985). Aspects of the trophic ecology of the mesopelagic fish *Lampanyctus alatus* (Family Myctophidae) in the eastern Gulf of Maine. Biol. Oceanogr. 3: 285–313

Jones, R. (1978). Estimates of the food consumption of haddock (*Melanogrammus aeglefinus*) and cod (*Gadus morhua*). J. Cons. int. Explor. Mer 38: 18–27

Kinzer, J., Schulz, K. (1985). Vertical distribution and feeding patterns of midwater fish in the central equatorial Atlantic. Mar. Biol. 85: 313–322

Kotlyar, A. N. (1980). Systematics and distribution of trachichthyid fishes (Beryciformes) of the Indian Ocean. Trudy Inst. Okeanol. Akad. Nauk SSR 110: 177–224

Kotlyar, A. N., Lipskaya, N. Y. (1980). Feeding of *Hoplostethus atlanticus* Collett (Trachichthyidae, Beryciformes). In: Fishes of the open ocean. Institute of Oceanology, Academy of Sciences USSR, Moscow, p. 89–93

Legand, M., Rivaton, J. (1969). Cycles biologiques des poissons mesopelagiques de l'est de l'ocean Indien. Troisieme note: action predatrice des poissons microectoniques. Cah. O.R.S.T.O.M., Sér. Oceanogr. 7: 29–45

Mace, M. M., Fenaughty, J. M., Coburn, R. P., Doonan, I. J. (1990). Growth and productivity of orange roughy (*Hoplostethus atlanticus*) on the north Chatham Rise. N.Z. J. mar. Freshwat. Res. 24: 105–119

Macpherson, E. (1981). Resource partitioning in a Mediterranean demersal fish community. Mar. Ecol. Prog. Ser. 4: 183–193

Marshall, N. B., Merrett, N. R. (1977). The existence of a benthopelagic fauna in the deep sea. Deep Sea Res. (Suppl.) 24: 483–497

Mauchline, J. (1988). Growth and breeding of meso- and bathypelagic organisms of the Rockall Trough, northeastern Atlantic Ocean and evidence of seasonality. Mar. Biol. 98: 387–393

Mauchline, J., Gordon, J. D. M. (1984). Occurrence and feeding of berycomorphid and percomorphid teleost fish in the Rockall Trough. J. Cons. int. Explor. Mer. 41: 239–247

Mauchline, J., Gordon, J. D. M. (1986). Foraging strategies of deep-sea fish. Mar. Ecol. Prog. Ser. 27: 227–238

Merrett, N. R., Roe, H. S. J. (1974). Patterns and selectivity in the feeding of certain mesopelagic fish. Mar. Biol. 28: 115–126

Morrow, J. E. Jr. (1964). Family Chauliodontidae. In: Bigelow, H. B. (ed.) Fishes of the western North Atlantic. Memoir, Sears Foundation for Marine Research, No. 1, part 4. Yale University, New Haven, p. 274–289

Olson, R. J., Mullen, A. J. (1986). Recent developments for making gastric evacuation and daily ration determinations. Envir. Biol. Fish. 16: 183–191

Pankhurst, N. W., Conroy, A. M. (1987). Size-fecundity relationships in the orange roughy, *Hoplostethus atlanticus*. N.Z. J. mar. Freshwat. Res. 21: 295–300

Roe, H. S. J. (1984). Vertical migration and feeding of mysids and decapod crustacea. Prog. Oceanog. 13: 269–318

Rosecchi, E., Tracey, D. M., Webber, W. R. (1988). Diet of orange roughy, *Hoplostethus atlanticus* (Pisces: Trachichthyidae) on the Challenger Plateau, New Zealand. Mar. Biol. 99: 293–306

Smith, K. L. Jr, Laver, M. B. (1981). Respiration of the bathypelagic fish Cyclothone acclinidens. Mar. Biol. 61: 261–266

Smith, M. M., Heemstra, P. C. (eds.) (1986). Smith's sea fishes. Springer-Verlag, Berlin

Tate, M. W., Clelland, R. C. (1957). Nonparametric and shortcut statistics in the social, biological and medical sciences. Interstate Printers and Publishers, Danville, Illinois

Torres, J. J., Belman, B. W., Childress, J. J. (1979). Oxygen consumption rates of midwater fishes as a function of depth of occurrence. Deep Sea Res. 26: 185–197

Vlieg, P. (1983). Transmission oil from fish? Catch (N.Z. Minist. Agric. Fish.) 10: 21–22

Ware, D. M. (1980). Bioenergetics of stock and recruitment. Can. J. Fish. Aquat. Sci. 37: 1012–1024

Young, J. W., Blaber, S. J. M. (1986). Feeding ecology of three species of midwater fishes associated with the continental slope of eastern Tasmania, Australia. Mar. Biol. 93: 147–156

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# CHAPTER 3

## Trophic ecology of the mid-slope demersal fish community off southern Tasmania, Australia

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# Trophic ecology of the mid-slope demersal fish community off southern Tasmania, Australia

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**Abstract.** We investigated the trophic structure of the demersal fish community on the mid-slope off southern Tasmania in southeastern Australia. This community is dominated by orange roughy *Hoplostethus atlanticus* (Trachichthyidae), several species of oreosomatids, macrourids, squalids, alepocephalids and a synaphobranchid eel. Cluster analysis based on diet dissimilarities of proportional prey weight identified five major trophic guilds: pyrosome-feeders, crustacean feeders, piscivores, benthopelagic omnivores, and benthic invertebrate feeders. Overall, the fish fed predominantly on pelagic or benthopelagic prey, consistent with other trophic studies in the Australasian region and the Northern Hemisphere. *H. atlanticus*, warty dory *Allocyttus verrucosus*, and the macrourid *Coryphaenoides serrulatus* were benthopelagic omnivores that ate mesopelagic fishes, crustaceans and squid. The first two species ate more mesopelagic fishes as their sizes increased. The squalids were predominantly piscivorous but might also scavenge. Macrourids were benthic invertebrate feeders, pelagic crustacean feeders or benthopelagic omnivores. The alepocephalids and the smooth oreo *Pseudocyttus maculatus* were pyrosome-feeders. No seasonal variation in diet was found for any species. Ecological indices varied within each guild. Benthopelagic omnivores and piscivores had the largest diet breadth, evenness, and diversity. Trophic levels ranged from 3.0 for pyrosome-feeders to 4.9 for piscivores and the overall average for the community was 3.7.

## Introduction

On the mid-slope (700-1200 m) off southeastern Australia, orange roughy *Hoplostethus atlanticus* (Trachichthyidae), dominates the demersal fish community (Koslow *et al.* 1994) and has been fished heavily since the late 1980's, particularly around several seamounts off eastern and southern Tasmania. Two other members of this mid-slope community, the smooth oreo *Pseudocyttus maculatus* and black oreo *Allocyttus niger*, have also become commercial targets since the orange roughy fishery has been restricted by catch limits. Exploitation of this community has stimulated scientific interest in the trophic mechanisms supporting fish production at these depths, including the trophic interactions between commercially exploited and non-commercial deepwater fish species.

The mid-slope community biomass is dominated by three families: Trachichthyidae *(H. atlanticus*, 23% of total biomass*)*, Oreosomatidae (oreos, 22%), and Squalidae (dogfishes, 20%) (Koslow *et al.* 1994). Other major families on the mid-slope were the Macrouridae (whiptails, 13%), Synaphobranchidae (basketwork eels, 8%) and Alepocephalidae (slickheads, 5%) (Koslow *et al.* 1994). Dietary studies of *H. atlanticus* found that they consume about 1% of their body weight per day (Bulman & Koslow 1992). Based on that estimate, a preliminary model developed by Koslow (1997) to assess energy flow through the water column off southern Tasmania, concluded that the aggregating species on the seamounts, such as *H. atlanticus*, were sustained by advection of resources from adjacent regions. However, the biomass of fish dispersed over the relatively flat parts of the seafloor could be supported by the productivity of the overlying water column. In a number of ecosystems around the world involving seamount and deep-water communities, it has been suggested that sufficient energy to sustain those communities is derived from the lateral advection of organisms past the seamounts or onto the slope from adjacent oceanic systems also (Isaacs and Schwartzlose 1965, Tseitlin 1985, Pereyra *et al.* 1969, Genin *et al.* 1988).

To understand the energy flow through the mid-slope community and to improve our models, we investigate here the trophic relationships and guild structure of the dominant species of the mid-slope demersal fish community off southern Tasmania, which included both seamount-associated and dispersed species. We investigated the dependence of fish predators on benthic or pelagic prey, and their

level of piscivory. Specifically, we described the diets of the dominant species and a variety of diet indices such as diet breadth, diet overlap and diversity. For species with sufficient data, we examined ontogenetic dietary shifts. Finally, we calculated trophic levels for species and constructed a simplified food web for the demersal fish community.

## Methods

*Study area*

The study site was located about 20 n miles south east of Pedra Branca, off southern Tasmania (Fig.1). The site first surveyed proved very difficult to trawl and another more trawlable site, 3 nautical miles southwest, was substituted during the following seasons. This area was bounded by 44° 09'S and 147° 04'E, and 44° 13'S and 147° 12'E. The bottom depth in this area was about 1000m and relatively flat compared to the surrounding terrain, which was comprised largely of seamounts.

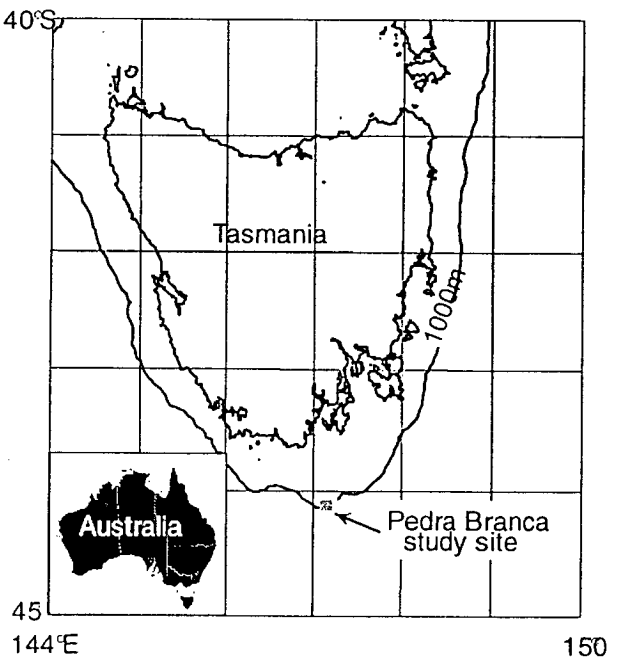



**Fig. 1.** Pedra Branca study site off southern Tasmania, Australia.

*Sampling*

The site was trawled during July 1991 (winter), February and November 1992 (summer and spring respectively), and April 1993 (autumn). During each seasonal survey, a series of demersal trawls was made over a 24-h period. A 35.5m headline Engel High-lift bottom trawl was used for all tows. Tows were made every 4 h and each tow was between 30 and 60 minutes duration. The fish caught were identified to species, weighed and counted. Biological information and stomachs were obtained for 23 species that were considered the dominant species of the community (see Table 3). A maximum of 20 stomachs per species per tow was collected. The stomachs were either frozen, or preserved in 4% formaldehyde if small. Specimens with everted stomachs or that had been obviously net-feeding were ignored.

*Laboratory analyses*

In the laboratory, prey items were identified to the lowest possible taxon, weighed after excess water was blotted off, and counted. They were then dried at 60°C and re-weighed. Diets were described in terms of proportion (%) of wet weight of prey and frequency of occurrence of prey initially. Dry weights of prey were converted to energy in kilojoules per gram of dry weight of prey ($kJg^{-1}$) using calorific data obtained in this study (Table 1) or from Bulman & Blaber (1986). Diets were expressed in terms of proportions of total dietary energy (%) of prey.

Identification of prey was made by every means possible. In the case of fishes, if otoliths were extracted from the remnant, we tried to identify them from our reference collections of otoliths and photographs. Occasionally fish were identified from their distinctive dentition. Crustacean remnants were identified from our reference collections of crustaceans or from literature. Similarly, cephalopods were identified from beaks based on a small reference collection. However, if hard parts were the only remains in the stomachs, they were noted but the stomach was assessed as empty.

**Table 1. Calorific values for some prey species from this study determined using bomb calorimetery.**

| Species | $kJ.g^{-1}$ | Mean per group |
|---|---|---|
| Pisces | | 21.95 |
| *Chauliodus sloani* | 21.15 | |
| *Tubbia tasmanica* | 31.89 | |
| *Bathylagus antarctica* | 21.10 | |
| *Bathylagus* sp. | 19.88 | |
| *Electrona paucirastra* | 19.24 | |
| *Electrona risso* | 20.68 | |
| *Metelectrona ventralis* | 22.42 | |
| *Howella* sp. | 16.82 | |
| *Symbolophorus barnardi* | 20.20 | |
| *Diretmus argenteus* | 19.68 | |
| *Idiacanthus atlanticus* | 21.94 | |
| *Icthyococcus* sp. | 25.38 | |
| *Woodsia* cf. *meyerhaardeni* | 22.21 | |
| *Diaphus hudsoni* | 20.94 | |
| *Diaphus danae* | 19.82 | |
| *Symbolophorus boops* | 24.50 | |
| *Lampanyctus ater* | 20.72 | |
| *Lampanyctus intracarius* | 23.66 | |
| *Lampanyctus australis* | 22.79 | |
| *Lampanyctus lepidolychnus* | 29.36 | |
| *Phosicthys argenteus* | 22.80 | |
| *Lampichthys procerus* | 21.11 | |
| *Persparsia kopua* | 22.03 | |
| *Coryphaenoides subserrulatus* | 20.04 | |
| *Coryphaenoides serrulatus* | 20.87 | |
| *Halargyreus johnstonii* | 20.10 | |
| *Hoplostethus atlanticus* | 28.44 | |
| *Caelorinchus matamua* | 20.40 | |
| *Caelorinchus kaiyomaru* | 20.18 | |
| *Deania calcea* | 28.05 | |
| *Centroscymnus crepidater* | 28.28 | |
| *Centroscymnus owstoni* | 31.84 | |
| Blubber (probably Cetacean) | 30.88 | |
| Crustacea (Natantia) | | 22.73 |
| *Pasiphae* sp. | 22.20 | |
| *Oplophorus novaezelandiae* | 23.41 | |
| *Notostomus* sp. | 30.03 | |

| Species | $kJ.g^{-1}$ | Mean per group |
|---|---|---|
| *Sergestes* sp. | 21.94 | |
| *Sergestes (Sergia) potens* | 21.94 | |
| *Acanthephyra quadrispinosa* | 20.32 | |
| *Gnathophausia* sp. | 21.07 | |
| *Sergia potens* | 19.30 | |
| Mollusca (Squid) | | 22.24 |
| Unidentified squid sp. 1 | 19.39 | |
| Unidentified squid sp. 2 | 22.81 | |
| Unidentified squid sp. 3 | 22.03 | |
| Unidentified squid sp. 4 | 22.87 | |
| *Histioteuthis* cf. *macrohista* | 23.61 | |
| Unidentified squid sp. 5 | 20.62 | |
| *Bathothauma* sp. | 24.86 | |
| *Leachia* sp. | 23.25 | |
| *Neoteuthis* sp. | 20.52 | |
| *Histioteuthis* sp. | 22.46 | |

**Table 2. Functional prey categories and major prey taxa, used to aggregate prey data in diet analyses of 23 fish species from the southern Tasmania.** Some taxa could have individual species in different functional groups.

| Functional group | Major taxa comprising functional groups |
|---|---|
| Benthic invertebrates | Echinodermata, Ectoprocta, Cnidaria, Gastropoda, Bivalvia, Holothuroidea |
| Polychaetes | Polychaeta |
| Benthic crustaceans | Isopoda, Gammaridae, Ostracoda |
| Megabenthos | Polychelidae, Reptantia |
| Benthic fish | Macrorhamphosidae, Moridae |
| Benthopelagic fish | Berycidae, Chimaeridae, Carangidae, Macrouridae, Moridae Squalidae, Synaphobranchidae |
| Pelagic fish | Bathylagidae, Bramidae, Ceratiidae, Chauliodontidae, Gonostomatidae, Idiacanthidae, Malacosteidae, Myctophidae, Neoscopelidae, Notosudidae, Phosicthyidae, Serrivomeridae, Stomiidae, Tetragonuridae |
| Pelagic invertebrates | Thaliacea, Teuthoidea |
| Pelagic crustaceans | Penaeidae, Sergestidae, Oplophoridae, Nematocarcinidae, Pandalidae, Pasiphaeidae, Rhynchocinetidae, Euphausiacea, Mysida, Calanoida, Hyperiidae |
| Pelagic mammals | Cetacea |
| Unknown fish | Unidentifiable fish remains |
| Unknown crustaceans | Unidentifiable crustacean remains |
| Unknown | Unidentifiable remains |

*Statistical analyses*

Prey taxa were amalgamated into 14 groups to allow a functional interpretation of the trophic interactions in the fish community (Table 2). This interpretation was compared with the analyses using all taxa. The functional categories were generally based on taxonomy and primary habitat except in the case of megabenthos, which comprised two phyla, Mollusca and Crustacea. The "unknown" crustacean and fish groups (Table 2) were pro-rated across the appropriate categories, assuming that the unidentified categories were spread proportionately across the known categories. A similar system was used by Fujita *et al.* (1995) when examining shelf fishes off northern Japan. Justification for categorisation was drawn from Last *et al.* (1983), Bulman and Blaber (1986), Blaber and Bulman (1987), and Bulman and Koslow (1992), Gomon *et al.* (1994) and Jones and Morgan (1994).

Seasonal variations in diet were tested using Kendall's coefficient of concordance, $W$ (Zar 1984), on the proportions by weight and by energy for prey groups, using the SPSS statistical package.

To determine the trophic guild structure, a hierarchical cluster analysis was performed on the weight data of prey for species that had more than 10 stomach samples. Bray-Curtis dissimilarities were calculated, from which a dissimilarity matrix was generated. An average linkage-clustering algorithm (UPGMA) was applied to generate the clusters using SPSS v 6.1 statistical package. Diet overlaps, $R$, between species pairs were calculated on the functional prey categories, $g$, using Schoener's (1968) overlap index, as used by MacPherson and Roel (1987), $R_{ih} = 1 - 0.5\sum_{g=1}^{N} | P_{ig} - P_{hg} |$, where $P_{ig}$ and $P_{hg}$ are the proportions of wet weight of prey category $g$ in species $i$ and $h$, and $N$ is total number of prey categories.

Species richness, $S$, is simply the number of prey species found in the diet of the predator and gives an indication of the richness of its diet but without any indication of the dominance or evenness of the prey species. Diet breadth, $D$, for each species was calculated from all prey taxa and from grouped prey taxa, using the Levins (1968) index as in Blaber and Bulman (1987), $D = (\sum_{g=1}^{N} P_g^2)^{-1}$, where $P_g$ is the

proportion by weight of each prey taxon or group, $g$, (Magurran 1983). Numbers of prey taxa or groups varied, so diet breadths were standardised to maximum breadths, *Max D,* using Hespenheide's (1975) method, $MaxD = (D-1)(N-1)^{-1}$, where $N$ is the number of prey taxa or categories eaten. This index is a measure of the dominance and is sensitive to changes in the abundance of the commonest species. Evenness, $E$, based on the Shannon index (Magurran 1983), was calculated so that $E = -\ln N^{-1} \sum_{g=1}^{N} P_g \ln P_g$. The reciprocal of the Berger-Parker index, $d^{-1}$, a dominance measure, was calculated: $d^{-1} = W_{\max}{}^{-1}.W_{\text{total}}$, where $W_{\max}$ is the weight of the largest prey category and $W_{\text{total}}$ is the total weight of prey. An increase in the index indicated an increase in diversity and reduction in dominance (Magurran 1983). Species that had less than 10 stomach samples were not included in the four preceding analyses.

Following the method used by Brodeur and Pearcy (1992) to describe the food web structure of a coastal pelagic system, we calculated the trophic level (TL) for the predator species of the mid-slope community and the averages for the guilds and overall community. Calculations were based on the trophic levels of prey taxa, $\text{TL}_g$, and their proportions in the diets of fish studied, $P_g$, so that, trophic level, $\text{TL} = 1 + \sum_{g=1}^{N} \text{TL}_g.P_g$. The trophic level of prey were assigned based on the hierarchy used by Mearns et al. (1981): primary producers =1; herbivores =2; primary carnivores=3; secondary carnivores=4; tertiary carnivores=5. We used similar assumptions about feeding habits. Small crustaceans, including copepods, mysids, ostracods, amphipods etc, were assumed to be herbivores even though many forms are not. Large crustaceans, including shrimps and prawns, mesopelagic fishes and cephalopods were assumed to be primary carnivores (3). Large piscivorous fishes were assumed to be secondary carnivores (4). The trophic level assignment procedure was used to position species in the food web. The results of these different approaches provided the basis on which a food web was constructed, to illustrate the major trophic links in the demersal fish community.

Changes in diet compositions with fish length were tested using the Mantel test (Mantel 1967, Manly 1994) for species that had more than 50 stomach samples: *H. atlanticus, Allocyttus verrucosus, Coryphaenoides subserrulatus, Caelorinchus*

*kaiyomaru* and *Synaphobranchus capensis.* The Mantel test is a randomized statistical method and its test statistic is the correlation between two matrices. The significance of the test statistic is determined by comparing it with the distribution of statistics obtained from randomly reallocating the order of the elements in one of the matrices a number of times. In our analysis, the first matrix, ***A***, was defined as the dissimilarity matrix of diet composition based on the functional prey groupings between all pairs of individual fish, or Schoener's overlap index. The second matrix, ***B***, was defined as the matrix of the differences in fish length between the pairs of individual fish. That is, for $n$ individual fish

$$A = \begin{bmatrix} 0 & & & \\ a_{21} & 0 & & \\ \cdots & \cdots & \cdots & \\ a_{n1} & a_{n2} & & 0 \end{bmatrix} \text{ and } B = \begin{bmatrix} 0 & & & \\ b_{21} & 0 & & \\ \cdots & \cdots & \cdots & \\ b_{n1} & b_{n2} & & 0 \end{bmatrix}$$

where $a_{ij} = 1 - R_{ij}$, $R_{ij}$ = Schoener's overlap index, $b_{ij} = |l_i - l_j|$, and $l_i$ and $l_j$ are lengths of fish $i$ and $j$. Because both matrices are symmetrical, the correlation between all the off-diagonal elements in two matrices is the same as the correlation between the $n(n-1)/2$ elements in the lower triangular diagonal parts. The correlation between the two matrices was compared to the distribution of the correlations calculated from randomly reallocating the elements of the ***B*** matrix 5,000 times. The values were ordered from smallest to greatest. The null hypothesis was that there were no differences in diet compositions between fish lengths and was rejected if the test statistic was greater than the 95$^{th}$ percentile of the ordered distribution of values. Fish were also grouped into size classes and graphed for visual inspection of diet variation by size.

## Results

*Diet description*

The majority of species fed predominantly on pelagic or benthopelagic prey (Tables 3 & 4). Myctophid fishes were the main prey for two squalids *Centroscymnus crepidater* and *Deania calcea*, blue grenadier *Macruronus novaezelandiae* and warty dory *A. verrucosus,* while bathylagid fishes contributed

most to the diet of *H. atlanticus*. Pelagic crustaceans such as carid and penaeid prawns also contributed to these species' diets. Smaller predator species, such as the macrourids, *Caelorinchus innotabilis* and *C. subserrulatus*, and the two cardinalfishes, *Epigonus* species, relied more heavily on the pelagic crustaceans. Benthic invertebrates, including polychaetes and crustaceans, constituted less than one third of the known diet in all species except the macrourid *C. kaiyomaru,* which ate predominantly benthic crustaceans and polychaetes. Benthic crustaceans constituted 25-30% of the diets of the macrourid *Caelorinchus kermadecus*, and of *C. innotabilis*. Gelatinous zooplankton (pelagic invertebrates), predominantly pyrosomes, was eaten almost exclusively by *Tubbia tasmanica* (Centrolophidae), *Tetragonurus cuvieri* (Tetragonuridae), the slickheads *Alepocephalus* species 1 and 2, and oreosomatids *Neocyttus rhomboidalis* and *P. maculatus*. Other pelagic invertebrates, i.e. squid, were eaten by *H. atlanticus*, *A. verrucosus*, *C. subserrulatus*, *C. serrulatus* (Macrouridae), most of the squalids, and basketwork eel *S. capensis.* Species that ate either gelatinous zooplankton or squid, components of the pelagic invertebrate category, became obvious from the cluster analysis. It distinguished all species that ate pyrosomes in large proportions from other species that ate squid (in significant proportions). For some species, prey items could not be well identified leaving large proportion of the diets only broadly classified.

Differences between composition by weight and energy were relatively small. Frequency of occurrence results often highlighted the difference between the indices when prey occurred commonly in stomachs but were relatively unimportant in their contribution to the diet in terms of weight or energy. For example, pelagic crustaceans occurred in about 60% of stomachs of *C. subserrulatus,* but contributed only 15% by weight or energy to the diet. Similarly, for *N. rhomboidalis*, pelagic crustaceans occurred in over 60% of stomachs, but contributed only half the energy and even less by weight. Fish prey generally contributed more in terms of energy than in terms of weight or frequency of occurrence. For instance, benthopelagic fish occurred in half the stomachs of the squalid *Centroscymnus owstoni* but contributed over 90% of the energy, highlighting the benefit of fish prey as an energy-dense food source. The occurrence of blubber (Cetacea) also had a large effect on the diet of the squalid *Centroscymnus coelolepis* in terms of energy.

There was a slight difference in diet in proportion of weight and of energy between seasons detected for *C. serrulatus*, but the difference was not significant. For half the species, there were not enough data to test and the other species showed no significant differences. Therefore, the dietary data for all surveys were combined to obtain an overall diet description for each species. The prey data were combined into functional groups (Table 3).

*Guild structure*

For the 12 species that had more than 10 stomach samples, the cluster analysis identified five trophic guilds based on functional prey groups (Fig. 2):

pyrosome-feeders: *Alepocephalus* sp. 1 and *Alepocephalus* sp. 2

pelagic crustacean feeders: *C. subserrulatus* and *Epigonus lenimen*

pelagic and benthopelagic piscivores: *D. calcea, C. crepidater, S. capensis* and *Etmopterus granulosus*

benthopelagic omnivores: *H. atlanticus, A. verrucosus* and *C. serrulatus*

benthic invertebrate feeder: *C. kaiyomaru.*

The dominant prey of each guild except the benthopelagic omnivores was indicated by the guild name (Table 3). The benthopelagic omnivores ate a wide range of prey including fish (Table 3). Based on data from our study and the literature, the remaining 11 species that had less 10 stomach samples, were tentatively assigned to trophic guilds:

pyrosome-feeders: *T. tasmanica, T. cuvieri, N. rhomboidalis and P. maculatus*

pelagic crustacean feeders: *C. innotabilis* and *Epigonus robustus*

pelagic and benthopelagic piscivores: M. *novaezelandiae, Macrourus carinatus, C. owstoni* and *C. coelolepis*

benthic omnivore: *C. kermadecus.*

**Table 3. Diet composition by wet weight (%), size range, numbers of samples and full stomachs, and mean stomach fullness per tow for 23 demersal fish species caught on the midslope (1000 m), near Pedra Branca, southern Tasmania.** Rare species have been collapsed into higher classification group where appropriate.

| Prey Species | *Coryphaenoides subserrulatus* | *Hoplostethus atlanticus* | *Alepocephalus* sp. 1 | *Allocytus verrucosus* | *Synaphobranchus capensis* | *Caelorinchus kaiyomaru* | *Centroscymnus crepidater* | *Alepocephalus* sp. 2 | *Etmopterus granulosus* | *Epigonus lenimen* | *Deania calcea* | *Coryphaenoides serrulatus* | *Centroscymnus coelolepis* | *Epigonus robustus* | *Caelorinchus innotabilis* | *Caelorinchus kermadecus* | *Neocytus rhomboidalis* | *Pseudocyttus maculatus* | *Centroscymnus owstoni* | *Macrourus novaezelandiae* | *Macrourus carinatus* | *Tubbia tasmanica* | *Tetragonurus cuvieri* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Size range (cm) | 13-42 | 11-43 | 17-70 | 13-40 | 28-138 | 17-33 | 20-98 | 16-65 | 21-82 | 11-22 | 30-118 | 24-49 | 88-95 | 12-19 | 20-33 | 25-55 | 24-43 | 16-56 | 70-112 | 72-93 | 98 | 29-53 | 39-50 |
| No stomachs examined | 339 | 402 | 124 | 99 | 263 | 59 | 79 | 77 | 70 | 27 | 25 | 15 | 11 | 7 | 5 | 5 | 11 | 19 | 6 | 4 | 1 | 4 | 18 |
| No full stomachs (n) | 257 | 175 | 92 | 70 | 51 | 50 | 43 | 38 | 27 | 13 | 10 | 10 | 6 | 5 | 3 | 3 | 3 | 3 | 2 | 1 | 1 | 1 | 1 |
| % stomachs with food | 76 | 44 | 74 | 71 | 19 | 85 | 54 | 49 | 39 | 48 | 40 | 67 | 55 | 71 | 60 | 60 | 27 | 16 | 33 | 25 | 100 | 25 | 6 |
| Mean fullness per tow | 2.03 | 1.81 | 4.62 | 6.85 | 4.75 | 4.30 | 1.79 | 2.29 | 10.94 | 0.65 | 1.01 | 3.92 | 12.17 | 2.77 | 2.02 | 1.85 | 1.43 | 0.20 | 7.98 | 0.36 | 29.02 | 0.27 | 5.77 |
| Ectoprocta (Coral) | - | - | - | - | - | - | - | 0.3 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Polychaeta | 0.4 | - | - | - | - | 43.5 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Crustacea | 73.9 | 24.3 | 0.3 | 29.1 | 0.8 | 52.9 | - | - | 2.4 | 94.1 | - | 43.7 | - | 100 | 100 | 58.7 | 11.6 | 14.7 | - | - | - | - | - |
| Calanoida | 5.2 | - | - | - | - | - | - | - | - | 68.5 | - | - | - | 97.5 | - | - | - | - | - | - | - | - | - |
| Other copepoda | 6.1 | 0.1 | - | - | - | - | - | - | - | 4.4 | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Mysida | 8.3 | 8.3 | - | 6.6 | 0.3 | 0.4 | - | - | 1.6 | - | - | 1.8 | - | - | - | - | 4.4 | - | - | - | - | - | - |
| Other amphipoda | 3.5 | 0.8 | - | 1.0 | - | 28.2 | - | - | - | - | - | 9.7 | - | - | - | 31.3 | - | - | - | - | - | - | - |
| Gammaridae | 0.4 | .2 | - | - | - | 12.8 | - | - | - | - | - | - | - | - | 26.5 | - | - | - | - | - | - | - | - |
| Penaeidae | 1.0 | 3.4 | - | - | - | 2.3 | - | - | - | - | - | 13.4 | - | - | 53.1 | - | - | - | - | - | - | - | - |
| Caridae | - | 6.7 | 0.3 | - | - | - | - | - | - | - | - | - | - | - | - | - | 7.2 | - | - | - | - | - | - |
| Reptantia | - | - | - | - | - | - | - | - | - | - | - | 6.5 | - | - | - | - | - | - | - | - | - | - | - |
| Polychelidae | - | - | - | - | - | - | - | - | - | - | - | 5.5 | - | - | - | - | - | - | - | - | - | - | - |
| Other crustacea | 49.4 | 5.0 | - | 21.5 | 0.5 | 9.6 | - | - | 0.8 | 21.1 | - | 6.8 | - | 2.5 | 20.4 | 27.4 | - | 14.7 | - | - | - | - | - |
| Mollusca | | | | | | | | | | | | | | | | | | | | | | | |
| Gastropods & bivalves | - | - | - | - | - | 0.7 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Teuthoidea | 1.8 | 7.5 | - | 16.6 | 02.9 | - | 3.7 | - | 9.2 | - | 1.6 | 7.9 | - | - | - | - | - | 14.7 | - | - | - | - | - |
| Holothuroidea | 0.1 | - | - | - | - | - | - | - | - | - | - | 2.2 | - | - | - | - | - | - | - | - | - | - | - |
| Thaliacea | 0.9 | 0.9 | 97.7 | 1.4 | - | - | - | 99.7 | - | 5.9 | - | 5.8 | - | - | - | - | 87.4 | 70.6 | 6.8 | - | - | 100.0 | 100.0 |
| Pisces | 22.4 | 67.3 | 2.0 | 52.9 | 94.2 | 1.8 | 95.7 | - | 88.4 | - | 98.4 | 40.3 | 87.6 | - | - | 41.3 | 1.0 | - | 93.2 | 100.0 | 100.0 | - | - |
| Squalidae | - | - | - | - | 20.3 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| *Bathylagus* sp. | - | 13.5 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| *Brama brama* | - | - | - | - | 40.2 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Ceratiidae | - | - | - | - | - | - | - | - | 21.1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| *Caelorinchus* sp. | 0.1 | 0.1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| *Coryphaenoides* species | - | 9.4 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 93.2 | - | 100.0 | - | - |
| *Chauliodus sloani* | - | 0.1 | - | 7.3 | - | - | 28.6 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| *Synaphobranchus capensis* | - | 1.5 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| *Hoplostethus atlanticus* | - | - | - | - | - | - | - | - | 10.1 | - | - | - | 52.7 | - | - | - | - | - | - | - | - | - | - |
| *Idiacanthus fasciola* | - | - | - | - | - | - | - | - | 3.7 | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| *Lampanyctus sp.* | - | 4.3 | - | - | - | - | 0.9 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| *Lampanyctus procerus* | - | - | - | - | - | - | 1.2 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| *Lampichthys australis* | - | - | - | - | 1.2 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Myctophidae (unid) | 11.0 | 3.4 | - | - | 0.4 | - | 3.6 | - | - | - | 41.3 | 2.0 | - | - | - | - | - | - | - | - | - | - | - |
| *Neoscopelus* sp. | - | 1.3 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| *Phosichthys argenteus* | - | - | - | - | - | - | 17.9 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| *Scopelosaurus* sp. | - | - | 1.9 | 5.2 | 0.7 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| *Serrivomer* sp. | - | - | - | - | - | - | 1.1 | - | 39.1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| *Trachurus declivis* | - | - | - | - | 0.8 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| *Tetragonurus cuvieri* | - | - | - | - | 1.0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Unid fish | 11.3 | 33.7 | 0.1 | 40.3 | 29.9 | 1.8 | 42.4 | - | 14.4 | - | 57.1 | 38.2 | 34.9 | - | - | 41.3 | 1.0 | - | - | 100.0 | - | - | - |
| Cetacea | - | - | - | - | - | - | - | - | - | - | - | - | 12.4 | - | - | - | - | - | - | - | - | - | - |
| Unidentified | 0.4 | - | - | - | 2.0 | 0.6 | 0.5 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |

**Table 4. Diet composition before pro-rating of 23 demersal fish species from mid-slope community off southern Tasmania.** Species are ordered by guilds.

| Predator | benthic invertebrate | polychaete | benthic crustacean | megabenthos | benthic fish | benthopelagic fish | pelagic crustacean | pelagic invertebrate | pelagic fish | marine mammal | unknown crustacean | unknown fish | unknown |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | % Energy | | | | | | | |
| *T. tasmanica* | - | - | - | - | - | - | - | 100.0 | - | - | - | - | - |
| *T. cuvieri* | - | - | - | - | - | - | - | 100.0 | - | - | - | - | - |
| *Alepocephalus* sp.2 | 4.2 | - | - | - | - | - | - | 95.8 | - | - | - | - | - |
| *Alepocephalus* sp.1 | - | - | - | - | - | - | 0.9 | 92.3 | 6.5 | - | - | 0.2 | - |
| *N. rhomboidalis* | - | - | - | - | - | - | 34.1 | 63.2 | - | - | - | 2.7 | - |
| *P. maculatus* | - | - | - | - | - | - | - | 74.7 | - | - | 25.3 | - | - |
| *E. lenimen* | - | - | - | - | - | - | 69.2 | 2.7 | - | - | 28.1 | - | - |
| *E. robustus* | - | - | - | - | - | - | 89.3 | - | - | - | 10.7 | - | - |
| *C. subserrulatus* | 0.1 | 0.4 | 2.7 | - | - | 0.1 | 14.7 | 1.2 | 13.8 | - | 56.0 | 10.6 | 0.5 |
| *C. innotabilis* | - | - | 26.4 | - | - | - | 52.6 | - | - | - | 21.0 | - | - |
| *D. calcea* | - | - | - | - | - | - | - | 0.2 | 51.4 | - | - | 48.4 | - |
| *M. novaezelandiae* | - | - | - | - | - | - | - | - | - | - | - | 100.0 | - |
| *C. crepidater* | - | - | - | - | - | - | - | 3.5 | 52.4 | - | - | 43.9 | 0.2 |
| *S. capensis* | - | - | - | - | - | 24.0 | 0.2 | 3.3 | 34.9 | - | 0.5 | 35.4 | 1.6 |
| *E. granulosus* | - | - | - | - | - | 22.6 | 1.7 | 8.6 | 47.5 | - | 0.8 | 18.9 | - |
| *M. carinatus* | - | - | - | - | - | 100.0 | - | - | - | - | - | - | - |
| *C. owstoni* | - | - | - | - | - | 98.9 | - | 1.1 | - | - | - | - | - |
| *C. coelolepis* | - | - | - | - | - | 42.5 | - | - | - | 42.2 | - | 15.3 | - |
| *H. atlanticus* | - | - | 0.7 | - | - | 7.9 | 16.6 | 6.2 | 28.3 | - | 3.5 | 36.8 | - |
| *A. verrucosus* | - | - | 1.4 | - | - | 5.4 | 6.0 | 14.2 | 7.5 | - | 20.7 | 44.7 | - |
| *C. serrulatus* | 1.2 | - | 6.4 | 9.3 | - | - | 13.0 | 9.0 | 2.7 | - | 7.2 | 51.2 | - |
| *C. kaiyomaru* | 2.7 | 47.0 | 34.5 | - | - | - | 3.8 | - | - | - | 9.9 | 1.6 | 0.6 |
| *C. kermadecus* | - | - | 12.4 | - | - | - | - | - | - | - | 10.4 | 77.2 | - |
| | | | | | | % Wet weight | | | | | | | |
| *T. tasmanica* | - | - | - | - | - | - | - | 100.0 | - | - | - | - | - |
| *T. cuvieri* | - | - | - | - | - | - | - | 100.0 | - | - | - | - | - |
| *Alepocephalus* sp.2 | 0.3 | - | - | - | - | - | - | 99.7 | - | - | - | - | - |
| *Alepocephalus* sp.1 | - | - | - | - | - | - | 0.3 | 97.7 | 1.9 | - | - | 0.1 | - |
| *N. rhomboidalis* | - | - | - | - | - | - | 11.6 | 87.4 | - | - | - | 1.0 | - |
| *P. maculatus* | - | - | - | - | - | - | - | 85.3 | - | - | 14.7 | - | - |
| *E. lenimen* | - | - | - | - | - | - | 68.5 | 5.9 | - | - | 25.5 | - | - |
| *E. robustus* | - | - | - | - | - | - | 97.5 | - | - | - | 2.5 | - | - |
| *C. subserrulatus* | 0.1 | 0.4 | 3.9 | - | - | 0.1 | 14.4 | 2.7 | 11.0 | - | 55.5 | 11.3 | 0.4 |
| *C. innotabilis* | - | - | 26.5 | - | - | - | 53.1 | - | - | - | 20.4 | - | - |
| *D. calcea* | - | - | - | - | - | - | - | 1.6 | 41.3 | - | - | 57.1 | - |
| *M. novaezelandiae* | - | - | - | - | - | - | - | - | - | - | - | 100.0 | - |

| Predator | benthic invertebrate | polychaete | benthic crustacean | megabenthos | benthic fish | benthopelagic fish | pelagic crustacean | pelagic invertebrate | pelagic fish | marine mammal | unknown crustacean | unknown fish | unknown |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *C. crepidater* | - | - | - | - | - | - | - | 3.7 | 53.3 | - | - | 42.4 | 0.5 |
| *S. capensis* | - | - | - | - | - | 20.3 | 0.3 | 2.9 | 44.3 | - | 0.5 | 29.9 | 2.0 |
| *E. granulosus* | - | - | - | - | - | 10.1 | 1.8 | 9.2 | 63.9 | - | 0.6 | 14.4 | - |
| *M. carinatus* | - | - | - | - | - | 100.0 | - | - | - | - | - | - | - |
| *C. owstoni* | - | - | - | - | - | 93.2 | - | 6.8 | - | - | - | - | - |
| *C. coelolepis* | - | - | - | - | - | 52.7 | - | - | - | 12.4 | - | 34.9 | - |
| *H. atlanticus* | - | - | 0.9 | - | - | 11.0 | 18.6 | 8.4 | 22.6 | - | 5.0 | 33.7 | - |
| *A. verrucosus* | - | - | 1.5 | - | - | - | 6.6 | 18.0 | 12.5 | - | 21.0 | 40.3 | - |
| *C. serrulatus* | 2.2 | - | 9.7 | 12.0 | - | - | 15.2 | 13.7 | 2.0 | - | 6.8 | 38.2 | - |
| *C. kaiyomaru* | 0.7 | 43.5 | 41.9 | - | - | - | 2.7 | - | - | - | 8.7 | 1.8 | 0.6 |
| *C. kermadecus* | - | - | 31.3 | - | - | - | - | - | - | - | 27.4 | 41.3 | - |
| | | | | | | % Frequency of occurrence | | | | | | | |
| *T. tasmanica* | - | - | - | - | - | - | - | 100.0 | - | - | - | - | - |
| *T. cuvieri* | - | - | - | - | - | - | - | 100.0 | - | - | - | - | - |
| *Alepocephalus* sp.2 | 2.60 | - | - | - | - | - | - | 97.4 | - | - | - | - | - |
| *Alepocephalus* sp.1 | - | - | - | - | - | - | 1.1 | 100.0 | 1.1 | - | - | 1.1 | - |
| *N. rhomboidalis* | - | - | - | - | - | - | 66.7 | 66.7 | - | - | - | 33.3 | - |
| *P. maculatus* | - | - | - | - | - | - | - | 100.0 | - | - | 33.3 | - | - |
| *E. lenimen* | - | - | - | - | - | - | 46.2 | 15.4 | - | - | 38.5 | - | - |
| *E. robustus* | - | - | - | - | - | - | 60.0 | - | - | - | 40.0 | - | - |
| *C. subserrulatus* | 0.4 | 1.6 | 3.9 | - | - | 0.4 | 18.0 | 3.5 | 2.30 | - | 67.7 | 16.0 | 0.8 |
| *C. innotabilis* | - | - | 33.3 | - | - | - | 33.3 | - | - | - | 66.7 | - | - |
| *D. calcea* | - | - | - | - | - | - | - | 10.0 | 30.0 | - | - | 60.0 | - |
| *M. novaezelandiae* | - | - | - | - | - | - | - | - | - | - | - | 100.0 | - |
| *C. crepidater* | - | - | - | - | - | - | 2.3 | 9.3 | 30.7 | - | - | 67.4 | 2.3 |
| *S. capensis* | - | - | 2.0 | - | - | 7.8 | 11.8 | 9.8 | 13.7 | - | 9.8 | 56.9 | 2.0 |
| *E. granulosus* | - | - | - | - | - | 7.4 | 11.1 | 22.2 | 11.1 | - | 3.7 | 51.9 | - |
| *M. carinatus* | - | - | - | - | - | 100.0 | - | - | - | - | - | - | - |
| *C. owstoni* | - | - | - | - | - | 50.0 | - | 50.0 | - | - | - | - | - |
| *C. coelolepis* | - | - | - | - | - | 16.7 | - | - | - | 33.30 | - | 66.7 | - |
| *H. atlanticus* | - | - | 11.4 | - | - | 7.4 | 44.0 | 8.5 | 7.4 | - | 22.9 | 24.0 | - |
| *A. verrucosus* | - | - | 7.1 | - | - | - | 22.9 | 24.3 | 2.9 | - | 57.1 | 45.7 | - |
| *C. serrulatus* | 10.0 | - | 10.0 | 40.0 | - | - | 30.0 | 30.0 | 10.0 | - | 30.0 | 60.0 | - |
| *C. kaiyomaru* | 10.0 | 62.0 | 82.0 | - | - | - | 6.0 | - | - | - | 24.0 | 2.0 | 4.0 |
| *C. kermadecus* | - | - | 33.3 | - | - | - | - | - | - | - | 66.7 | 33.3 | - |

*Diet overlap*

Within each guild, diet overlaps were high (Fig. 3) as in the pyrosome feeders (>0.9), the squalids (pelagic-benthopelagic piscivores) (>0.7) and the benthopelagic omnivores (>0.7). The benthopelagic omnivores overlapped moderately with the squalids (0.4-0.6) and with *C. subserrulatus* (~0.5).

*Ecological indices*

In general, the piscivores, omnivores, and benthic invertebrate feeders had broader and more diverse diets than pyrosome-feeders and pelagic crustacean-feeders (Table 5). The benthopelagic omnivores had the broadest, most even and most diverse diets. However, index values varied considerably between species within each guild (Table 5). For some species, indices also changed depending on whether all prey taxa were used or whether prey were grouped by functional category.

Within the guild of pyrosome feeders, the diets of the two alepocephalids, which ate mostly pyrosomes, were understandably very narrow in breadth, Max$D$, very low in species richness, $S$, evenness, $E$, and diversity, $d^{-1}$, regardless of how the prey were grouped (Table 5).

Within the guild of pelagic crustacean feeders, the indices varied widely. *C. subserrulatus* had the narrowest diet breadth also with a midrange of diet diversity. The indices of *E. lenimen* changed considerably when prey were grouped by functional category: diet narrowed, and evenness and diversity declined markedly (Table 5).

Within the guild of pelagic and benthopelagic piscivores, indices also varied widely: the diets of two pelagic piscivores, *C. crepidater* and *D. calcea* were more even and diverse than those of the two benthopelagic piscivores, *S. capensis* and *E. granulosus*. Indices for the two pelagic piscivores also declined dramatically when prey taxa were grouped by functional category, while indices for the two benthopelagic piscivores remained relatively similar (Table 5).

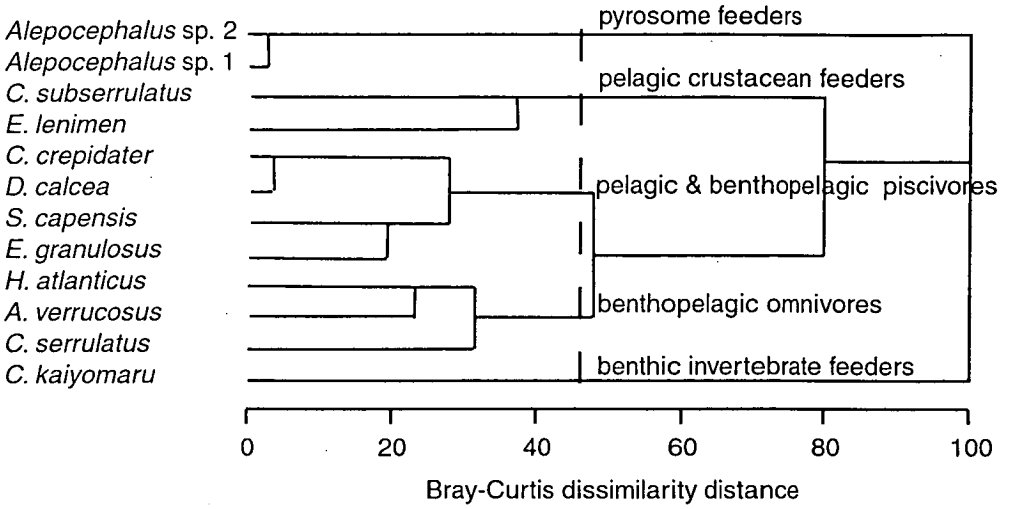



**Fig 2**. Dendrogram from cluster analysis of 12 demersal fish species showing five major trophic guilds of demersal fishes off southern Tasmania based on functional grouping of wet weight of prey. The vertical dashed line indicates the level of dissimilarity that separates the species into the 5 trophic guilds.

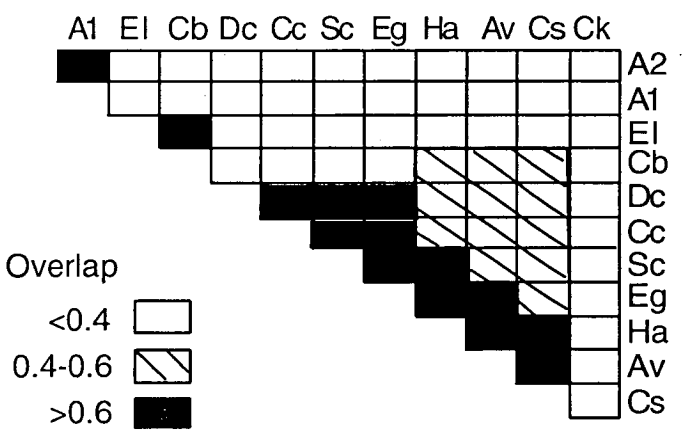



**Fig. 3.** Dietary overlap of 12 demersal species off southern Tasmania based on functional groups of wet weight of prey. Species legend: A1=*Alepocephalus* sp. 1, A2=*Alepocephalus* sp. 2, El=*Epigonus lenimen*, Cb=*Coryphaenoides subserrulatus*, Dc=*Deania calcea*, Cc=*Centroscymnus crepidater*, Sc=*Synaphobranchus capensis*, Eg=*Etmopterus granulosus*, Ha=*Hoplostethus atlanticus*, Av=*Allocyttus verrucosus*, Cs=*Coryphaenoides serrulatus*, Ck=*Caelorinchus kaiyomaru*.

**Table 5. Ecological indices of the diets, and trophic levels (TL) of demersal fish species from the midslope off southern Tasmania.** Indices were calculated only where n≥10. Species are grouped into 5 guilds. Symbols are: $N$ = number of stomach samples; TL = trophic level; $S$ = species richness; Max $D$= maximum diet breadth; $E$ = evenness; and $d^{-1}$ = Berger-Parker dominance. Subscripts, *all* and *fg*, indicates that calculations use all prey taxa or prey grouped by functional category, respectively. * Guild assumed.

| Guild/Species | $N$ | TL | $S_{all}$ | $S_{fg}$ | Max $D_{all}$ | Max $D_{fg}$ | $E_{all}$ | $E_{fg}$ | $d^{-1}{}_{all}$ | $d^{-1}{}_{fg}$ |
|---|---|---|---|---|---|---|---|---|---|---|
| Pyrosome-feeders | | | | | | | | | | |
| *T. tasmanica* | 1 | 3.0 | - | - | - | - | - | - | - | - |
| *T. cuvieri* | 1 | 3.0 | - | - | - | - | - | - | - | - |
| *Alepocephalus* sp. 2 | 38 | 3.0 | 2 | 2 | 0.01 | 0.01 | 0.03 | 0.03 | 1.00 | 1.00 |
| *Alepocephalus* sp. 1 | 92 | 3.0 | 4 | 3 | 0.02 | 0.02 | 0.09 | 0.11 | 1.02 | 1.02 |
| *N. rhomboidalis* | 3 | 3.1 | - | - | - | - | - | - | - | - |
| *P. maculatus* | 3 | 3.3 | - | - | - | - | - | - | - | - |
| Pelagic crustacean-feeders | | | | | | | | | | |
| *E. lenimen* | 13 | 3.2 | 6 | 2 | 0.50 | 0.12 | 0.78 | 0.32 | 2.70 | 1.06 |
| *E. robustus* | 5 | 3.0 | - | - | - | - | - | - | - | - |
| *C. subserrulatus* | 257 | 3.8 | 19 | 8 | 0.14 | 0.20 | 0.60 | 0.53 | 2.02 | 1.71 |
| *C. innotabilis* | 3 | 3.7 | - | - | - | - | - | - | - | - |
| Pelagic and benthopelagic piscivores | | | | | | | | | | |
| *D. calcea* | 10 | 4.3 | 3 | 2 | 0.51 | 0.03 | 0.68 | 0.12 | 1.75 | 1.02 |
| *M. novaezelandiae* | 1 | 4.5 | - | - | - | - | - | - | - | - |
| *C. crepidater* | 43 | 4.2 | 10 | 4 | 0.26 | 0.03 | 0.63 | 0.14 | 2.36 | 1.04 |
| *S. capensis* | 51 | 4.7 | 16 | 6 | 0.17 | 0.20 | 0.57 | 0.49 | 2.49 | 1.56 |
| *E. granulosus* | 27 | 4.2 | 10 | 4 | 0.35 | 0.22 | 0.72 | 0.56 | 2.56 | 1.32 |
| *M. carinatus* | 1 | 4.0 | - | - | - | - | - | - | - | - |
| *C. owstoni* | 2 | 3.9 | - | - | - | - | - | - | - | - |
| *C. coelolepis* | 6 | 4.5 | - | - | - | - | - | - | - | - |
| Benthopelagic omnivores | | | | | | | | | | |
| *H. atlanticus* | 175 | 4.1 | 29 | 5 | 0.20 | 0.54 | 0.72 | 0.80 | 2.97 | 2.21 |
| *A. verrucosus* | 70 | 4.1 | 9 | 4 | 0.38 | 0.52 | 0.75 | 0.77 | 2.48 | 1.89 |
| *C. serrulatus* | 10 | 4.0 | 11 | 6 | 0.41 | 0.61 | 0.83 | 0.87 | 2.62 | 2.50 |
| Benthic invertebrate feeder | | | | | | | | | | |
| *C. kaiyomaru* | 50 | 3.1 | 12 | 6 | 0.22 | 0.25 | 0.61 | 0.55 | 2.30 | 2.00 |
| Benthic omnivore* | | | | | | | | | | |
| *C. kermadecus* | 3 | 3.9 | - | - | - | - | - | - | - | - |

Within the guild of the benthopelagic omnivores, the diets of *H. atlanticus, A. verrucosus* and *C. serrulatus* actually broadened and evenness increased when prey taxa were grouped by functional category while the diversity of their diets decreased only slightly. The diet of *H. atlanticus* was initially the most diverse before grouping but *C. serrulatus* was the most diverse after grouping.

Within the guild of benthic invertebrate feeders, indices for *C. kaiyomaru* were quite similar to those of the benthopelagic piscivore and the pelagic crustacean feeder guilds: diet breadth was narrow, evenness was mid-range and diversity was relatively high, none of which declined much when prey was grouped (Table 5).

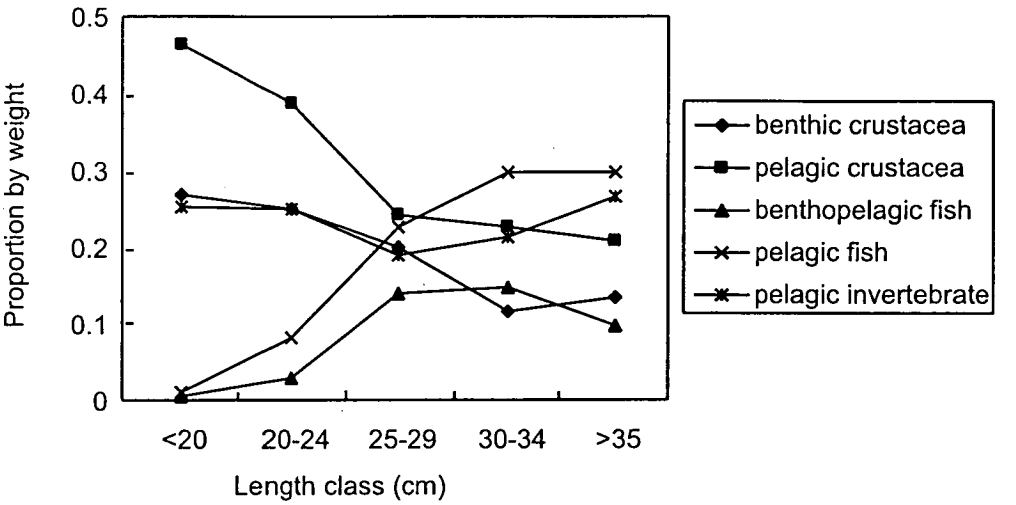
The few data for *C. kermadecus* indicated that it was a benthic omnivore (Table 5).

*Trophic level assignments*

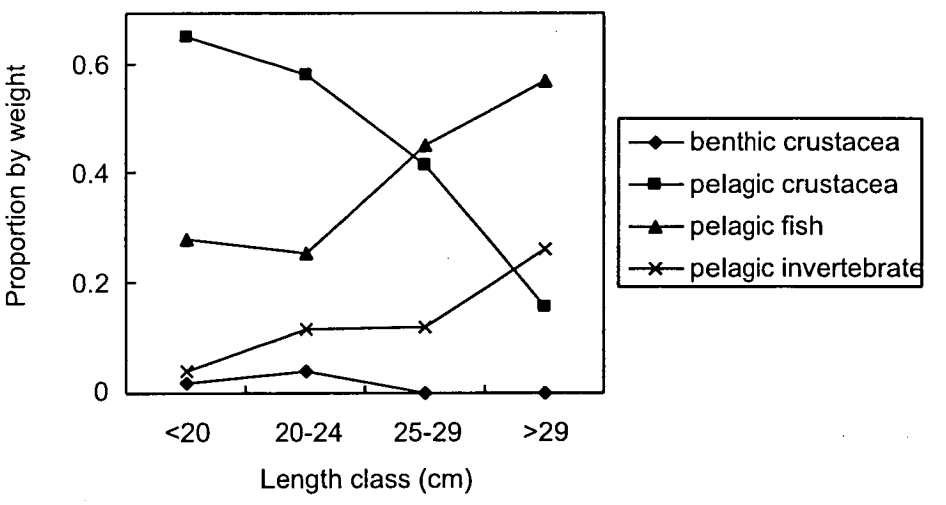
Trophic levels varied between 3.0 and 4.9 for individual species (Table 5), the highest being for piscivores: *C. coelolepis* (4.9), *S. capensis* (4.7) and *M. novaezelandiae* (4.5). The average TL of the pyrosome feeders was 3; that of the pelagic crustacean feeders was 3.5; that of the benthopelagic omnivores was 4.1 and that of the pelagic and benthopelagic piscivores was the highest at 4.4. An overall average of TL for the community was 3.7 if each species was weighted equally on its consumption level.

*Dietary variations with size*

Diet changed with size in two of the five species tested, *H. atlanticus* and *A. verrucosus*. With increasing size, the proportion by weight of crustaceans declined in the diet of *H. atlanticus*, while that of fish, particularly pelagic, increased (Mantel test $p = 0.015$)(Fig. 4a). Similarly, as *A. verrucosus* increased in size, the proportions by weight of fish and squid (pelagic invertebrate) increased, that of pelagic crustaceans decreased (Fig. 4b) and those of pyrosomes were constant (Mantel test $p=<0.001$). Both these species were sampled over a size range from sub-adult to adult. The tests on the other species showed no significant trends, which might have been due to either insufficient data or too narrow a size range to detect variations in diets.




(a) *Hoplostethus atlanticus*




(b) *Allocyttus verrucosus*

**Fig. 4.** Size variation in diet by proportional wet weight of prey for (a) *Hoplostethus atlanticus* and (b) *Allocyttus verrucosus* caught off southern Tasmania.

## Discussion

Overall, the diets of the major demersal mid-slope fishes off southern Australia are dominated by pelagic or benthopelagic prey. In terms of energy, fish was generally the most significant prey, highlighting its benefit as an energy-dense food source and its role in transporting energy into deeper water. Similar results were found for fishes of the upper- and mid-slope and abyssal plains in the Atlantic Ocean (Marshall and Merrett 1977, Sedberry and Musik 1978, DuBuit 1978, Mauchline and Gordon 1983, 1984 a, b, c, Houston and Haedrich 1986, Gordon and Mauchline 1990), the upper slope off Oregon (Pearcy and Ambler 1974) and on the upper slope of south-eastern Australia and New Zealand (Bulman and Blaber 1986, Blaber and Bulman 1987, Clark *et al.* 1989). In the Rockall Trough in the North Atlantic, 76 of the 110 fish species, including the dominant species, ate predominantly benthopelagic prey and to a lesser extent epibenthic prey (Gordon and Mauchline 1990). In the demersal fish community off North West Africa, mesopelagic or bathypelagic prey were important and off West Africa, benthopelagic or pelagic prey were most important (Marshall and Merrett 1977). This is in contrast with the less productive waters off Western Australia, where the biomass of demersal species was several-fold lower and benthic feeders predominated (Williams *et al.* 2001).

*H. atlanticus* ate fish, prawns and squid consistent with large diet studies of *H. atlanticus* in south-eastern Australia (Bulman & Koslow 1992), New Zealand (Rosecchi *et al.* 1988) and north-eastern Atlantic (Mauchline and Gordon 1984 a). The most-favoured fish prey, from the identifiable component, was a bathylagid species that could not be further identified. *Melanolagus bericoides*, a bathylagid, was amongst the most abundant micronektonic fish in the water column in our study area (Williams and Koslow 1997). Bathylagids were also prominent in the diets of both juvenile and adult roughy caught off western Tasmania, the Great Australian Bight (Bulman and Koslow 1992) and off New Zealand (Rosecchi *et al.* 1989). The *Coryphaenoides* species were also dominant prey species that were caught regularly in demersal and midwater trawls (this study, Williams and Koslow 1997) and were some of the most abundant species of the mid-slope (Koslow *et al.* 1994). Myctophids including *Lampanyctus* species in particular, comprised nearly 10% of prey, and were very abundant in the micronekton in the water column (48.5%: Williams and Koslow 1997). These prey fishes were all found in the deeper strata of

the water column most commonly where they would be vulnerable to predation by *H. atlanticus* and other benthopelagic predators, swimming up into the water column to feed.

Adult *A. verrucosus,* also abundant in the deeper mid-slope region (Koslow *et al.* 1994), ate mostly fish, crustaceans and squid, similar to an earlier study of this species in the South African sub-region (Mel'nikov 1980). It ate the most abundant micro-nektonic species in the study area, such as *Chauliodus sloani* and *Scopelosaurus* species (Williams and Koslow 1997). The other important oreo occurring in our area, *P. maculatus*, ate mostly the gelatinous zooplankton species, *Pyrosoma* sp., and in New Zealand, it ate mostly salps (Clark *et al.* 1989).

Several large species besides *P. maculatus* also fed largely on gelatinous zooplankton: *N. rhomboidalis, T. tasmanica, T. cuvieri* and the *Alepocephalus* species. Consistent with our results, *N. rhomboidalis* on the upper slope off Tasmania ate 35% salps, including *Pyrosoma* species (Blaber and Bulman 1987). *T. cuvieri* was reported to eat ctenophores and coelenterates and that the young were associated with medusae (Grey 1955 and references therein). No dietary information for *T. tasmanica* was available. Gelatinous zooplankton, mostly pyrosomes, comprised a high proportion of micronekton catches in the study area - ~60% (Williams and Koslow 1997), providing a substantial food source for these species.

Vinogradov and Tseitlin (1983) hypothesized that larger fish that are more energetic usually ate the higher-calorie, migratory prey. Interestingly, several of our large, energetic species ate only gelatinous zooplankton, a relatively low-calorie prey. However, this prey was also exclusively eaten by the less energetic, but similarly-sized, *Alepocephalus* species. These species have more watery flesh than the two oreos and apparently lower metabolic requirements (Chapter 4).

The macrourids exhibited a range of feeding behaviours from benthopelagic piscivory to benthic invertebrate feeding. Apart from *C. kaiyomaru*, the macrourids were apparently quite dependent on pelagic sources of prey, consistent with diet investigations and habits of many macrourids in the North Pacific (Pearcy and Ambler 1974), North Atlantic (Haedrich and Henderson 1974, Pearcy 1976, Sedberry and Musick 1978, Smith 1978, Mauchline and Gordon 1984 b, 1991) and New Zealand (Clark *et al.* 1989). Large macrourids, such as *Coryphaenoides*

*armatus* from the North Atlantic, make extensive migrations up into the water column to prey on the mesopelagic *Chauliodus sloani* (Haedrich and Henderson 1974). Indeed, *C. subserrulatus* were caught at least 100m off bottom in midwater trawls in our study area (Williams and Koslow 1997). In contrast to the pelagic habit of most macrourids off south-eastern Australia, Williams *et al.* (2001) observed, based on morphological evidence, that benthic feeding macrourids dominated off the Western Australian coast. These differences appear to be related to the lower water-column production off Western Australia.

Two of the five species of Squalidae examined were probably scavenging. *C. coelolepis* ate blubber, probably cetacean, although it was impossible to determine whether from a dead or live animal. Mauchline and Gordon (1983) also found cetacean fragments in stomachs from this species from the northeastern Atlantic. However, over half its diet was orange roughy. The other squalid *E. granulosus,* also ate orange roughy, accounting for one-fifth of the energy in the diet. It was not possible to determine conclusively whether these occurrences of orange roughy were a result of net feeding, scavenging discarded catches or normal predation. However, we note that *E. granulosus* attains a maximum length of 62 – 75 cm (Last and Stevens 1994), only slightly larger than the orange roughy, and predation is less likely.

The squalids *Centroscymnus crepidater* and *Deania calcea* fed on the abundant mesopelagic prey species in the study area (Williams and Koslow 1997), and their diets were similar to those from the North Atlantic (Marshall and Merrett 1977, Mauchline and Gordon 1983). Their specialized feeding on mesopelagic species, such as *C. sloani* or myctophids suggests that they also swim into the water column to feed in layers where these particular species are aggregated (Williams and Koslow 1997).

There appear to be at least two general ecological strategies for deepwater benthopelagic species feeding on meso- and bathypelagic prey off southern Tasmania: pursuit of prey into the water column, as shown by

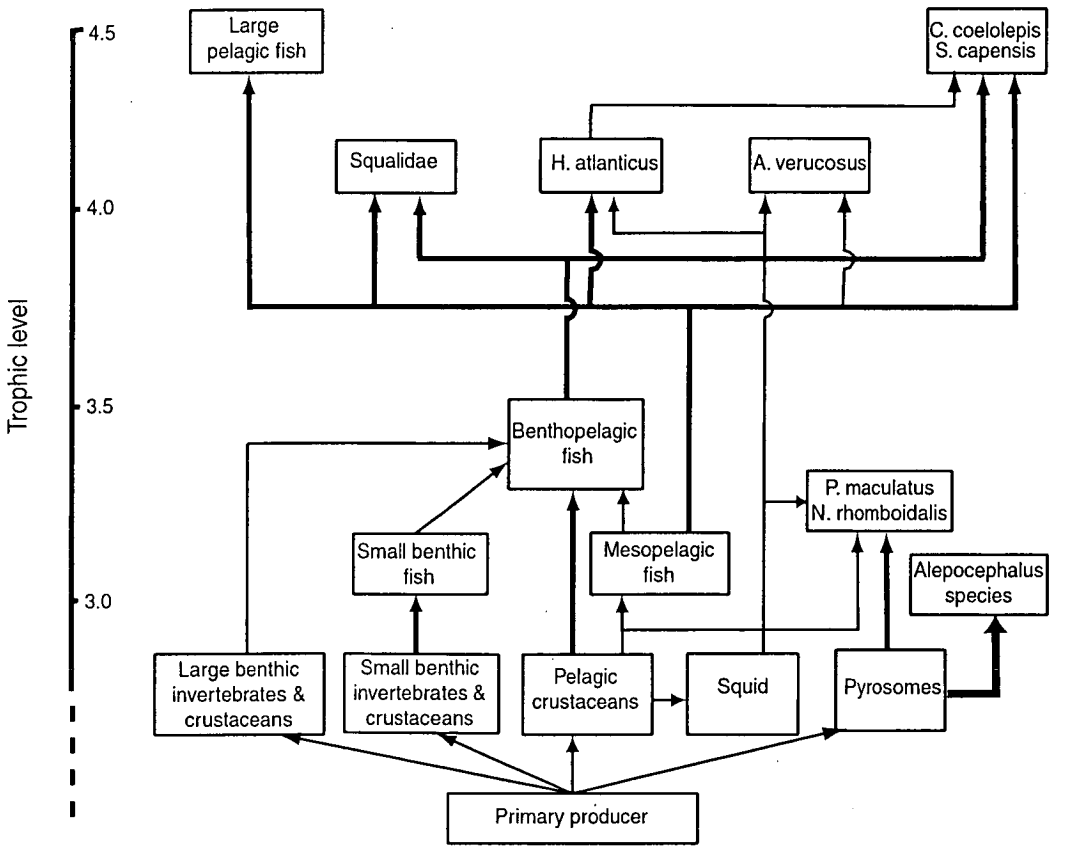



**Fig. 5.** Food web diagram of the major trophic groups of the mid-slope community off southern Tasmania, and their interactions. Thick lines indicate greater level of contribution. Higher order species and groups are placed approximately by trophic level but lower order groups are not due to complexity of the species mixes they contain.

*Coryphaenoides* species and many squalids (Haedrich and Henderson 1974, Gordon and Mauchline 1990); and aggregation on banks and seamounts, as shown by orange roughy, *Sebastes* species, and the pelagic armorhead, all of which depend on horizontal advection or the interception of vertical migrators (Isaacs and Schwartzlose 1965, Marshall and Merrett 1977, Genin *et al.* 1988, Mauchline and Gordon 1991, Gordon *et al.* 1995). Although we did not sample directly on seamounts, ~90% of the Tasmanian orange roughy stock is found on seamounts (Koslow *et al.* 1994), and simple trophodynamic models indicate that allochthonous input to such limited topographic features is necessary to support substantial deepwater aggregations (Tseitlin 1985, Koslow 1997).

High levels of diet overlap were found within guilds and moderate levels between some species of different guilds, consistent with results obtained on the upper slope by Blaber and Bulman (1987). Merrett and Haedrich (1997) attributed high diet overlaps between fishes of relatively productive shelf and upper slope regions such as ours, particularly within guilds and within closely related species, to an excess of resources in those regions. This observation might extend to the mid-slope depths.

The data were too few enough to allow a more complete investigation of ecological diversity parameters, however some generalities could be made. Diets of guild members generally became more diverse as benthopelagic sources of prey increased and as diets became omnivorous. The least diverse guilds were reliant on very few sources of pelagic prey. These ecological considerations might be fundamental to the way in which fish species respond to fishing pressures or other environmental impacts.

In any dietary study, grouping data and pro-rating unknown groups will usually result in a reduction of diversity that might not be helpful if competition or diversity is examined, but is informative when examining the overall functioning of an "ecosystem". Our approach covered both angles, but interpretation of the structure of the demersal fish community was our main objective, which the functional approach better provides. Consequently, the cluster analysis was based on functional groups and thus the guilds identified reflect the overall structure of our system. The combination of results from these different approaches provided the basis from

which to construct a simplified food web of the demersal community on the slope (Fig. 5). The "top" predators in our community were the squalids, *H. atlanticus* and *A. verrucosus*. These species were all highly reliant on benthopelagic and mesopelagic food sources, indeed, as were the majority of species investigated. Interestingly, whereas size is often correlated with trophic level, the pyrosome feeders were of similar size to the orange roughy and oreos, yet were at a markedly lower trophic level. *C. coelolepis* and *S. capensis* had the highest trophic level because they ate marine mammals or fishes of a high trophic level respectively, although the relative roles of predation and scavenging here are unclear. This region experienced periods of intensive fishing, when discarding and incidental mortality was greater, therefore the incidence of scavenging might also have increased relative to the ecosystem's pristine state. The information that we provide here will serve as a basis for further investigation of the mid-slope ecosystem off southeastern Australia, and its fishery.

**Acknowledgments**

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## References

**Blaber, S. J. M., and Bulman, C. M.** (1987). Diets of fishes of the upper continental slope of eastern Tasmania: content, calorific values, dietary overlap and trophic relationships. *Marine Biology* **95**: 345-356.

**Brodeur, R. D., and Pearcy, W. G.** (1992). Effects of environmental variability on trophic interactions and food web structure in a pelagic upwelling ecosystem. *Marine Ecology Progress Series* **84**:101-119.

**Bulman, C. M., and Blaber, S. J. M.** (1986). The feeding ecology *of Macruronus novaezelandiae* (Hector, 1871) (Teleostei: Merluciidae) in south-east Australia. *Australian Journal of Marine and Freshwater Research* **37**: 243-247.

**Bulman, C. M., and Koslow, J. A.** (1992). Diet and food consumption of a deep-sea fish, orange roughy, *Hoplostethus atlanticus* (Pisces: Trachichthyidae), off southeastern Australia. *Marine Ecology Progress Series* **82**: 115-129.

**Clark, M.R., King, K. J., and McMillan, P. J.** (1989). The food and feeding relationships of black oreo, *Allocyttus niger*, smooth oreo, *Pseudocyttus maculatus*, and eight other fish species from the continental slope of the south-west Chatham Rise, New Zealand. *Journal of Fish Biology* **35**: 465-484.

**DuBuit, M. H.** (1978). Alimentation de quelques poissons téléostéens de profondeur dans la zone du seuil de Wyville Thomson. *Oceanologica Acta* **1**: 129-134.

**Fujita, T., Kitagawa, D., Okuyama, Y., Ishito, Y., Inada, T., and Jin, Y.** (1995). Diets of the demersal fishes on the shelf off Iwate, northern Japan. *Marine Biology* **123**: 219-233.

**Genin, A., Haury, L., and Greenblatt, P.** (1988). Interactions of migrating zooplankton with shallow topography: predation by rockfishes and intensification of patchiness. *Deep-Sea Research* **35**: 151-175.

**Gomon, M. F., Glover, J. C. M., and Kuiter, R. H.** (1994). 'The Fishes of Australia's South Coast.' (State Print: Adelaide, Australia).

**Gordon, J. D. M., and Mauchline, J.** (1990). Depth-related trends in diet of a deep-sea bottom-living fish assemblage of the Rockall Trough. In 'Trophic Relationships in the Marine Environment.' (Eds M. Barnes and R. N. Gibson) pp. 439-452. (University Press: Aberdeen.)

**Gordon, J. D. M., Merrett, N. R., and Haedrich, R. L.** (1995). Environmental and biological aspects of slope-dwelling fishes of the North Atlantic. In 'Deepwater Fisheries of the North Atlantic Oceanic Slope.' (Ed. A. G. Hopper.) pp. 1-26. (Kluwer Academic Publishers: Netherlands).

**Grey, M.** (1955). The fishes of the genus *Tetragonurus* Risso. *Dana-Reports Carlsberg Foundation* **41**: 1-46.

**Haedrich, R. L., and Henderson, N. R.** (1974). Pelagic food of *Coryphaenoides armatus*, a deep benthic rattail. *Deep-Sea Research* **21**: 739-744.

**Hespenheide, H. A.** (1975). Prey characteristics and predator niche width. In 'Ecology and Evolution of Communities.' (Eds M. L. Cody and J. M. Diamond.) pp. 158-180. (Belknap Press: Cambridge, Mass.)

**Houston, K.A., and Haedrich, R. L.** (1986). Food habits and intestinal parasites of deep demersal fishes from the upper continental slope east of Newfoundland, northwest Atlantic Ocean. *Marine Biology* **92**: 563-574.

**Isaacs, J. D., and Schwartzlose, R. A.** (1965). Migrant sound scatterers: interaction with the sea floor. *Science* **150**: 1810-1813.

**Jones, D. S., and Morgan, G. J.** (1994). 'A Field Guide of Crustaceans of Australian Waters.' (Reed: Chatswood, Australia.)

**Koslow, J. A., Bulman, C. M., and Lyle, J. M.** (1994). The mid-slope demersal fish community off southeastern Australia. *Deep-Sea Research* **41**: 113-141.

**Koslow, J. A.** (1997). Seamounts and the ecology of deep-sea fisheries. *American Scientist* **85**: 168-176.

**Last, P. R., Scott, E. O. G., and Talbot, F. H.** (1983). 'Fishes of Tasmania.' (Tasmanian Fisheries Development Authority: Hobart, Australia.)

**Last, P. R., and Stevens, J. D.** (1994). 'Sharks and Rays of Australia.' (CSIRO: Australia.) 513 pp.

**Levins, R.** (1968). 'Evolution in Changing Environments: Some Theoretical Explorations.' (Princeton University Press: Princeton, N. J.)

**MacPherson, E., and Roel, B. A.** (1987). Trophic relationships in the demersal fish community off Namibia. In 'The Benguela and Comparable Ecosystems.' (Eds A. I. L. Payne, J. A. Gulland and K. H. Brink.) *South African Journal of Marine Science* **5**: 585-596.

**Magurran, A.** (1983). 'Ecological Diversity and its Measurement.' (Croom Helm: London.)

**Manly, B. F. J.** (1994). 'Randomization and Monte Carlo Methods in Biology.' (Chapman and Hall: London.)

**Mantel, N.** (1967). The detection of disease clustering and a generalized regression approach. *Cancer Research* **27**: 209-220.

**Marshall, N. B., and Merrett, N. R.** (1977). The existence of a benthopelagic fauna in the deep-sea. In 'A Voyage of Discovery. George Deacon 70$^{th}$ Anniversary Volume.' Supplement to Deep-Sea Research and Oceanographic Abstracts.(Ed. M. V. Angel.) pp 483-497. (Pergamon Press: UK.)

**Mauchline, J., and Gordon, J. D. M.** (1983). Diets of the sharks and chimaeroids of the Rockall Trough, northeastern Atlantic Ocean. *Marine Biology* **75**: 269-278.

**Mauchline, J., and Gordon, J. D. M.** (1984 a). Occurrence and feeding of berycomorphid and percomorphid teleost fish in the Rockall Trough. *Journal du Conseil International pour l' Exploration de la Mer* **41**: 239-247

**Mauchline, J., and Gordon, J. D. M.** (1984 b). Diets and bathymetric distributions of the macrourid fish of the Rockall Trough, northeastern Atlantic Ocean. *Marine Biology* **81**: 107-121.

**Mauchline, J., and Gordon, J. D. M.** (1984 c). Feeding and bathymetric distribution of the gadoid and morid fish of the Rockall Trough, northeastern Atlantic Ocean. *Journal of the Marine Biological Association UK* **64**: 657-665.

**Mauchline, J., and Gordon, J. D. M.** (1991). Oceanic pelagic prey of benthopelagic fish in the benthic boundary layer of a marginal oceanic region. *Marine Ecology Progress Series* **74**: 109-115.

**Mearns, A. J., Young, D. R., Olson, R. J., and Schafer, H. A.** (1981). Trophic structure and the cesium-potassium ration in pelagic ecosystems. *California Cooperative Oceanic Fisheries Investigations Report* **22**: 99-110.

**Mel'nikov, Y. S.** (1980). Feeding peculiarities of *Allocyttus verrucosus*, Family Oreosomatidae. *Journal of Ichthyology* **20**: 99-105.

**Merrett, N. R., and Haedrich, R. L.** (1997). 'Deep-Sea Demersal Fish and Fisheries.' (Chapman & Hall: London.)

**Pearcy, W. G., and Ambler, J. W.** (1974). Food habits of deep-sea macrourid fishes off the Oregon coast. *Deep-Sea Research* **21**: 745-759.

**Pearcy, W. G.** (1976). Pelagic capture of abyssobenthic macrourid fishes off the Oregon coast. *Deep-Sea Research* **21**: 745-759.

**Pereyra, W. T., Pearcy, W. G., and Carvey, F. E.** (1969). *Sebastodes flavidus*, a shelf rockfish feeding on mesopelagic fauna, with consideration of the ecological implications. *Journal of Fisheries Research Board Canada* **26**: 2211-2215.

**Rosecchi, E., Tracey, D. M., and Webber, W. R.** (1988). Diet of orange roughy, *Hoplostethus atlanticus* (Pisces: Trachichthyidae) on the Challenger Plateau, New Zealand. *Marine Biology* **99**: 293-306.

**Sedberry, G. A., and Musick, J. A.** (1978). Feeding strategies of some demersal fishes of the continental slope and rise off mid-Atlantic coast of the USA. *Marine Biology* **44**: 357-375.

**Schoener, T. W.** (1968). The *Anolis* lizards of Bimini: resource partitioning in a complex fauna. *Ecology* **49**: 704-726.

**Smith, K. L.** (1978). Metabolism of the abyssopelagic rattail *Coryphaenoides armatus* measured *in situ*. *Nature* **274**: 362-364.

**Tseitlin, V. B.** (1985). Energetics of fish populations inhabiting seamounts. *Oceanology* **25**: 237-239.

**Vinogradov, M. E., and Tseitlin, V. B.** (1983). Deep-sea pelagic domain (Aspects of bioenergetics). In 'Deep Sea Biology.' The Sea, Vol 8. (Ed. G. T. Rowe.) pp.123-165. (John Wiley & Sons: New York.)

**Williams, A., and Koslow, J. A.** (1997). Species composition, biomass and vertical distribution of micronekton over the mid-slope region off southern Tasmania, Australia. *Marine Biology* **130**: 259-276.

**Williams, A., Koslow, J. A., and Last, P.** (2001). Diversity, density and community structure of the demersal fish fauna of the continental slope off western Australia (20-35°S). *Marine Ecology Progress Series* **212**:247-263.

**Zar, J. H.** (1984). 'Biostatistical Analysis.' (Prentice Hall: New Jersey.)

# CHAPTER 4

## Enzyme activities and related ecology of eight demersal fishes from the mid-slope (700-1200 m) off Tasmania, southeastern Australia.

*Environmental Biology of Fishes*
(Submitted October 2001)
Co-author: J. A. Koslow

# Enzyme activities and related ecology of eight demersal fishes from the mid-slope (700-1200 m) off Tasmania, southeastern Australia.

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**Abstract.** We assayed lactate dehydrogenase (LDH), malate dehydrogenase (MDH) and citrate synthase (CS) activities of white muscle of eight demersal fish in the mid-slope demersal community off southern Australia. These eight species represented most of the biomass and a cross-section of the locomotory and trophic guilds in this community. They included two seamount-associated species: orange roughy, *Hoplostethus atlanticus*, and smooth oreo, *Pseudocyttus maculatus*. They were all anaerobically poised, with LDH activities greater than CS activities. The LDH activities of adult *Pseudocyttus maculatus*, *Centroscymnus crepidater* and *Hoplostethus atlanticus* were higher than the majority of deep-living species studied previously. CS in *H. atlanticus* and *A. verrucosus* scaled significantly and the scaling coefficients were similar to the generalised scaling coefficient of -0.26 for mass-specific aerobic metabolism. Oxygen consumption for *H. atlanticus*, estimated from a total energy budget including food consumption rate (Bulman and Koslow 1992), was compared to data from other studies which correlated $O_2$ consumption rates with enzyme activities. $O_2$ consumption for *H. atlanticus* did not fit any relationship for demersal fishes particularly well. The relationships between enzyme activities and oxygen consumption for the group of seamount-associated fish, in which orange roughy belongs, might fall somewhere between the pelagic and demersal relationships.

*Keywords:* metabolism, seamount-associated fish, oxygen consumption rates

## Introduction

In a recent review, Koslow (1996) suggested that deep-sea demersal and benthopelagic fishes were organised into two distinct guilds; fish that were associated with topographic features such as seamounts and fish that were dispersed over the sea floor. The species that aggregate around the seamounts were more robust and considered to have greater locomotory ability, partly to account for the greater energy required to maintain themselves in stronger currents associated with these features. Around seamounts off southern Australia, these species include the orange roughy, *Hoplostethus atlanticus*, smooth oreo, *Pseudocyttus maculatus,* and black oreo, *Allocyttus niger*, all of which are caught commercially in depths greater than 600m. Studies of their feeding and food consumption have suggested that roughy are quite energetic and possess a higher metabolic rate than other deepwater demersal fishes (Bulman and Koslow 1996, Koslow 1997).

The seamount-associated fishes are not obligate seamount dwellers and can be found dispersed over the seafloor (Koslow *et al.* 1994). The two families, to which these species belong, Trachichthyidae and Oreosomatidae, constitute nearly half of the biomass of the fish fauna on the relatively flat portions of the mid-slope around southeastern Australia (Koslow *et al.* 1994). However, fishery landings and surveys suggest that 90% of the *H. atlanticus* stock resides on seamounts, probably elevating the species to the most dominant fish species by mass in those communities (Koslow *et al.* 1994). In contrast, orange roughy is not a dominant member of the demersal fish community in the North Atlantic although small commercial landings have been made off France (Charuau *et al.* 1995), around seamounts of the mid-Atlantic Ridge (Troyanovsky and Lisovsky 1995) and the Faeroe Islands (Merrett and Haedrich 1997).

The species that disperse over the seafloor are usually either sit-and-wait predators or ones that slowly cruise. They include the macrourids whose elongate tapered morphology suggests the latter lifestyle. The Macrouridae constitute a further 13% of biomass of the mid-slope fish fauna around southeastern Australia (Koslow *et al.* 1994). The Squalidae is also a dominant family of this community (20% biomass: Koslow *et al.* 1994). It includes benthopelagic scavengers and predators

(Bulman *et al.* 2002). Alepocephalidae contribute 5% to the biomass of the community. They are sit-and-float predators without swim bladders and feed largely on pelagic tunicates (Gartner *et al.* 1997). Benthopelagic species that achieve neutral buoyancy through low-density body fluids such as these and the ophidids are considered some of the most energy-efficient fishes in the deep-sea (Crabtree 1995).

Koslow *et al.* (1994) hypothesised that, based on the density and food consumption rate of orange roughy, primary productivity in the overlying water column would be sufficient to support the biomass of this species on the open seafloor but not sufficient to support the higher concentrations on the seamounts. To examine this hypothesis in relation to the demersal community as a whole, we sought methods to estimate the energetic requirements of the dominant fish species.

Deepwater species are difficult to maintain for routine metabolic measurements based on respiration. However Childress and Somero (1979) suggested that enzyme activities might be good predictors of metabolic rate in situations where respiration cannot be directly measured. They derived relationships between oxygen consumption rates and lactate dehydrogenase (LDH) and malate dehydrogenase (MDH) activities for small pelagic species. Torres and Somero (1988a) derived a relationship between oxygen consumption and citrate synthase (CS) activity for a variety of species. Yang and Somero (1993) derived relationships between CS activities and oxygen consumption rates for *Sebastolobus alascanus* and *S. altivelis*, deep- and shallow-living scorpaenids of southern California. They also concluded that CS activities might provide the best estimates of whole-fish metabolism. Similar correlations were found in deep-sea worms (Childress and Thuesen 1992, Thuesen and Childress 1993) but investigations of metabolic rate and enzyme activity in deep-sea copepods failed to find significant relationships (Thuesen *et al.* 1998).

Early studies on pelagic deep-sea fishes and crustaceans found that their respiration rates were lower than those of shallower species and that respiration rates generally declined rapidly with increasing depth of occurrence (Smith and Hessler 1974, Smith 1978, Smith and Laver 1981, Smith and Brown 1983, Childress and Somero 1979, Torres *et al.* 1979, Cowles *et al.* 1991). However, this decline in respiration or metabolic rate is not ubiquitous and has not been found in groups such

as the pelagic chaetognaths, cnidarians, worms and pteropods (Childress 1995), nor in benthic crustaceans (Childress *et al.* 1990, Childress and Mickel 1985) and deep-sea copepods (Thuesen *et al.* 1998).

Childress and Somero (1979) found that enzyme activity of white muscle of pelagic fishes off southern California also decreased with increasing depth of occurrence. They concluded that this decrease represented a reduction in enzyme metabolism. In a wider study of shallow- and deep-living fishes, Sullivan and Somero (1980) found a similar association of declining enzyme activities in white muscle with increasing depth. They correlated LDH activities of a group of fishes from a narrow depth range with feeding and locomotory habits. Thuesen *et al.* (1998) used enzyme ratios of LDH and CS to interpret lifestyle patterns of deep-sea copepods.

In this paper, we examine LDH, MDH and CS activities of white muscle of eight demersal fishes in the mid-slope demersal community off southern Australia, including two seamount species: orange roughy *Hoplostethus atlanticus,* and smooth oreo *Pseudocyttus maculatus.* These eight species represent most of the biomass and a cross-section of the types of locomotory and feeding habits in this community, as well as representing the two guilds of fishes categorised by Koslow (1996). We examine their enzyme activities in relation to what is known of their lifestyles and locomotory patterns and compare them with the activities of species from earlier studies. The relationships between enzyme activities and oxygen consumption rates of a range of species from the earlier studies were also re-examined. Oxygen consumption for *H. atlanticus*, estimated from a total energy budget including food consumption rate (Bulman and Koslow 1992), was compared to the data from these studies.

## Methods

*Field collection of samples*

The study site was located south of Tasmania bounded by 44° 09'S and 147° 04'E, and 44° 13'S and 147° 12'E. The bottom depth in this area was about 1000m and relatively flat compared to the surrounding terrain comprised largely of

seamounts, and a major orange roughy fishing ground. Samples were collected during April 1993 (autumn). Demersal trawls were carried out over a period of about 24 h. Tissue samples for enzyme assays were collected from eight species: orange roughy *Hoplostethus atlanticus*, smooth oreo *Pseudocyttus maculatus*, warty oreo *Allocyttus verrucosus* (found on the lower slopes of seamounts and the sea floor), long-rayed whiptail *Coryphaenoides subserrulatus*, serrulate whiptail *C. serrulatus*, small-scaled slickhead Alepocephalus sp. 1, large-scaled slickhead *Alepocephalus* sp. 2, and golden *dogfish Centroscymnus crepidater.*

Size scaling of enzyme activity and metabolic rate is a well-known phenomenon (Peters 1983, Somero and Childress 1980, 1985, 1990; Childress and Somero 1990) so, where possible, a range of sizes was collected for each species. After capture, fish to be sampled were kept in icy seawater until processed. About one cubic cm of white muscle tissue was cut from behind the pectoral fin and blast-frozen at -30°C. Frozen tissues were stored at -70°C on return to the laboratory.

In addition, three specimens of *H. atlanticus* and four of *P. maculatus* were collected in December 1995 from the Cascade Plateau, southeast of Tasmania (43° 57'S, 150° 28'E). On capture, these fish were immediately frozen and stored in a domestic freezer (-10°C), and returned to the laboratory within 48 h. Tissues were excised immediately while still frozen and stored at -70°C. They were assayed within seven days of capture.

*Tissue preparation*

About 0.3g of frozen tissue was homogenised on ice with four times the volume of 0.1M Tris-HCl (pH 7.5 @10°C). Homogenates were centrifuged at 2500g for 10 minutes at 0°C. The supernatant was pipetted off and kept on ice during the assays. 400 $\mu$l of the homogenate were kept frozen for protein analyses.

Samples were assayed in a GBC-UV 910 spectrophotometer with a water-cooled thermostat cell-holder. The temperature of the assays was kept at 10° ± 1°C. The substrate mixtures were incubated at 9°C. They stabilised rapidly to 10°C in the cuvette before the addition of the enzyme.

*Assays*

*Lactate dehydrogenase LDH (E. C. 1.1.1.27)*

LDH regulates the final step in anaerobic metabolism (glycolysis), the process of energy production in the absence of oxygen. This type of metabolism is used only when short burst of power is required (<20 seconds), such as for prey capture or avoiding danger, because muscle reserves of glycogen are very limited. This method is much less efficient than aerobic metabolism, therefore the capacity for glycolysis and the levels of enzymes associated with glycolysis would have to be high in animals that are active and rely on this method of energy production in white muscle (Crabtree and Newsholme 1972). During burst activity, lactate accumulates in the white muscle and re-oxidises post-exercise via the aerobic pathway resulting in an oxygen debt. This oxygen debt may take several hours to repay and oxygen consumption will remain raised during this period (Jobling 1994). This is the reason why LDH activities might act as a predictor for metabolic rates (Hochachka and Somero 1984).

LDH was assayed in a medium of 80 mM Tris-HCl, 162 $\mu$M NADH, 100 mM KCl and optimal concentration of Na-pyruvate at 10°C. Concentrations of Na-pyruvate of 10, 50, 100, 500, 1000 and 5000 $\mu$M were tested for each species to determine the concentration at which an optimal velocity of reaction occurred. 10 $\mu$l of the supernatant was added to 2 ml of the substrate medium and the decrease in absorbance was recorded at 340 nm for 4 minutes. Three replicates of each sample were assayed.

*Malate dehydrogenase MDH (E. C. 1.1.1.37)*

MDH isozymes are involved in several reactions: in the citric acid cycle, in shuttling reducing equivalents between mitochondria and cytoplasm, and in maintenance of the redox balance of white muscle (Childress and Somero 1979). Because of its multiplicity of roles, MDH is not considered as good an indicator of burst activity as LDH (Siebenaller *et al.* 1982).

MDH was assayed in a medium of 40mM Tris-HCl, 40mM $MgCl_2$, 500 $\mu$m Na-pyruvate, 100mM KCl and 162$\mu$M NADH at a pH 8.1 at 10°C. Oxaloacetic acid concentration varied from 0.2mM to 0.4mM according to species. A 25$\mu$l aliquot of supernatant was added to 2 ml of the substrate and the decrease in absorbance at 340nm was recorded for 4 minutes. Three replicates of each sample were assayed.

*Citrate synthase CS (E. C. 4.1.3.7)*

CS is a regulatory enzyme in first step of the citric acid cycle where energy is produced under aerobic conditions. Fish that can maintain sustained activity for long periods (>200 minutes) use energy via the aerobic system. Station holding in midwater, foraging at low speed and long-distance migrations are classified as sustained activities (Jobling 1994). Prolonged swimming is an activity of shorter duration than sustained swimming (20 seconds to 200 minutes) but it eventually results in fatigue. It uses energy from both systems. In white muscle CS levels are relatively low, reflecting the tissue's anaerobic potential (Siebenaller *et al.* 1982).

50 ul of the supernatant was incubated at 9°C in a medium of 50 mM imidazole-HCl, 1.5 mM $MgCl_2$, 0.1 mM DNTB, and 0.1 mM acetyl-CoA for at least 20 minutes. This mixture was transferred to the cuvette and monitored for 1 minute at 412 nm to establish background activity of oxaloacetate in the supernatant. 25 $\mu$l of an optimal concentration of oxaloacetate were added and the increase in absorbance was recorded for a further seven minutes. Concentrations of oxaloacetic acid of 0.1, 0.5, 1.0, 4.0 and 8.0 $\mu$M were tested for each species to determine optimal concentrations.

*Protein analyses*

Protein was determined using a Sigma Protein Assay Kit (P5656) based on Peterson's modification of the micro-Lowry method. The samples to be tested were thawed and rehomogenated. Because Tris was the substrate in the samples, proteins were precipitated first. Calibration curves were run before each batch of samples.

*Water content*

About 1 g of muscle tissue was dried at 60°C for 24 h. Water content as percentage wet weight was calculated from the difference in weights before and after drying

*Data analyses*

For each species, mass-specific enzyme activity was regressed against weight to determine the scaling coefficients, *a* and *b*. The mean activity for each enzyme was calculated, and for *H. atlanticus*, *P. maculatus* and *A. verrucosus*, mean activities for juveniles were also calculated. Units are number of moles substrate converted per minute per g wet weight of muscle tissue ($Ug^{-1}$) as in Childress and Somero (1979).

The enzyme activities and the oxygen consumption for *H. atlanticus* (0.14 l $O_2$ $kg^{-1}$: Bulman and Koslow 1992) were compared with those for species from earlier studies. The relationships of LDH or MDH, and oxygen consumption for 32 and 24 species respectively, using data of Childress and Somero 1979 and additional data (see Table 1), were calculated by regressing log-transformed enzyme activities and consumption rates. Similarly, the relationship between CS and oxygen consumption for 24 Antarctic and Californian species was calculated, using the data of Torres and Somero (1988a) corrected to 10°C and additional data (see Table 1). Oxygen consumption rates were routine rates therefore that of *H. atlanticus* was halved to approximate a routine or resting rate. Wherever temperature corrections were necessary the data were corrected using the formula of Schmidt-Nielsen (1979, p. 208) and assuming a $Q_{10}$ =2.

The data for *H. atlanticus* were then statistically tested using studentised residuals (Minitab Manual 1996) to determine whether they fit the relationships derived from the large data sets. Using the derived relationships, oxygen consumption rates were estimated for *H. atlanticus*, based on its enzyme activities, and compared to the original estimate of Bulman and Koslow (1992).

**Table 3. Data used in lactate dehydrogenase (LDH), malate dehydrogenase (MDH) and citrate synthase (CS) vs. oxygen consumption relationships.** Enzyme activities ($Ug^{-1}$ wet wt) and oxygen consumption rates ($\mu l\ mg^{-1}h^{-1}$) at 10°C. MDO = minimum depth of occurrence. Data for Hoplostethus atlanticus was not used in the derivation of relationships.

| Species | MDC | Av. Wt (g) | LDH | MDH | CS | $VO_2$ | Reference |
|---|---|---|---|---|---|---|---|
| *Engraulis mordax* | 0 | 8.7 | 540.0 | 61.0 | 1.5 | 0.110 | Sullivan and Somero 1980 |
| *Pagothenia borghgrevinki* | 0 | 61 | 93.6 | | 2.3 | 0.307 | Torres and Somero 1988a,b |
| *Gillichthys mirabilis* | 5 | ~200 | 321.0 | 26.0 | 0.9 | 0.023 | Sullivan and Somero 1980 |
| *Symbolophorus californiensis* | 10 | 2.9 | 188.1 | 24.6 | | 0.085 | Childress and Somero 1979 |
| *Tarletonbeania crenularis* | 10 | 1.3 | 385.0 | 86.8 | | 0.186 | Childress and Somero 1979 |
| *Scorpaena guttata* | 20 | 1000 | 337.5 | 8 | 0.5 | 0.011 | Yang and Somero 1993 |
| *Leuroglossus stilbius* | 25 | 8.3 | 45.0 | 8.1 | 0.8 | 0.034 | Childress and Somero 1979 |
| *Triphoturus mexicanus* | 25 | 1.8 | 46.1 | 22.1 | 0.7 | 0.067 | Childress and Somero 1979 |
| *Bathylagus wesethi* | 25 | 6.1 | 83.6 | 9.3 | | 0.095 | Childress and Somero 1979 |
| *Trematomus bernacchi* | 30 | 148 | 106.3 | | 1.6 | 0.110 | Torres and Somero 1988 |
| *Electrona antarctica* | 50 | 4.5 | 50.1 | | 2.2 | 0.081 | Torres and Somero 1988b |
| *Lampanyctus ritteri* | 75 | 4.9 | 31.0 | 8.9 | 1.0 | 0.059 | Childress and Somero 1979 |
| *Gymnoscopelus opisthopterus* | 150 | 17.8 | 23.1 | | 0.9 | 0.043 | Torres and Somero 1988b |
| *Gymnoscopelus braueri* | 150 | 8.2 | 14. | | 1.2 | 0.050 | Torres and Somero 1988b |
| *Anoplopoma fimbria* | 200 | 1500 | 107 | 16 | 0.48 | 0.015 | Sullivan and Somero 1980 |
| *Stomias atriventer* | 300 | 33.2 | 7.9 | 3.2 | | 0.040 | Childress and Somero 1979 |
| *Sebastolobus altivelis* | 350 | 139 | 26.4 | 3.5 | 0.2 | 0.005 | Smith and Brown 1983 |
| *Trematomus loenbergii* | 350 | 106 | 75 | | 1.65 | 0.100 | Torres and Somero 1988 |
| *Poromitra crassiceps* | 400 | 14.1 | 4.8 | 2.0 | | 0.017 | Childress and Somero 1979 |
| *Bathylagus antarcticus* | 400 | 14 | 14.0 | | 0.4 | 0.035 | Torres and Somero 1988b |
| *Rhigophila dearborni* | 400 | 32.6 | 207.0 | | 1.5 | 0.035 | Torres and Somero 1988a,b |
| *Sebastolobus alascanus* | 500 | 250 | 57.0 | 3.7 | 0.3 | 0.008 | Yang and Somero 1993 |
| *Lampanyctus regalis* | 500 | 25.7 | 12.4 | 2.1 | | 0.016 | Childress and Somero 1979 |
| *Cyclothone microdon* | 500 | 1.0 | 374.0 | | 0.4 | 0.031 | Torres and Somero 1988b |
| *Cyclothone acclinidens* | 500 | 1.0 | 13.6 | | 0.6 | 0.034 | Torres and Somero 1988b |
| *Borostomias panamensis* | 500 | 118 | 1.1 | 2.8 | 0.3 | 0.033 | Childress and Somero 1979 |
| *Bathylagus milleri* | 550 | 39.4 | 7.2 | 2.3 | 0.09 | 0.016 | Childress and Somero 1979 |
| *Melanonus zugmayeri* | 550 | 89 | 57.2 | 6.4 | | 0.024 | Childress and Somero 1979 |
| *Anoplogaster cornuta* | 550 | 50.8 | 18.9 | 5.0 | | 0.034 | Childress and Somero 1979 |
| *Scopelengys tristis* | 650 | 37.4 | 6.2 | 1.6 | | 0.013 | Childress and Somero 1979 |
| *Parvilux ingens* | 700 | 20.7 | 12.3 | 3.6 | | 0.017 | Childress and Somero 1979 |
| *Oneirodes acanthias* | 900 | 130 | 8.1 | 1.4 | | 0.011 | Childress and Somero 1979 |
| *Bajacalifornia burragei* | 1000 | 31.9 | 7.8 | 1.4 | 0.4 | 0.007 | Childress and Somero 1979 |
| *Coryphaenoides acrolepis* | 1230 | 1800 | 154.0 | 9.0 | 0.31 | 0.004 | Smith and Brown 1983 |
| *Coryphaenoides armatus* | 2753 | 344 | 53.1 | 18.5 | 0.79 | 0.005 | Smith and Brown 1983, Siebenaller 1984 |
| *Hoplostethus atlanticus* adult | 700 | 1920 | 98 | 6.0 | 0.14 | 0.070 | This study |
| *Hoplostethus atlanticus* juv | 700 | 430 | 31.3 | 2.7 | 0.21 | 0.055 | This study |

## Results

*Enzyme activities and scaling*

*P. maculatus* had the highest LDH activity of all the adult fish at 163 $Ug^{-1}$ followed by *C. crepidater* (108 $Ug^{-1}$) and *H. atlanticus* (98 $Ug^{-1}$) (Table 2). *A. verrucosus* LDH activity was midway between this group and a group with very low activities containing *Coryphaenoides* species and *Alepocephalus* species (4-31 $Ug^{-1}$). The effect of body size on enzyme activity was clear in *H. atlanticus* where LDH activity increased significantly with increasing size (Table 3, Figure 1). The LDH regressions for *H. atlanticus*, *A. verrucosus* and *C. subserrulatus* were all positive and significant, but those for *P. maculatus* and *Alepocephalus* sp. 1 were not significant (Table 3).

The highest level of MDH was found in *P. maculatus* adults and juveniles (13 and 11 $Ug^{-1}$ respectively). The two *Coryphaenoides* species, *H. atlanticus* and *A. verrucosus* formed an intermediate group between 6-9 $Ug^{-1}$. The Alepocephalids had the lowest MDH activities (2-3 $Ug^{-1}$). *Alepocephalus* sp. 1 scaled positively but not significantly. MDH activity in *H. atlanticus* scaled positively and significantly, $b$=0.48 (Table 3, Figure 2). MDH in *C. subserrulatus* also scaled positively but not quite significantly. MDH in *P. maculatus* and *A. verrucosus* did not scale.

The *Coryphaenoides* species had the highest CS activities, (1.25 and 0.73 $Ug^{-1}$), being several times higher than the other fish but they were also the smallest of the fishes and would be expected to have higher CS activities. However juveniles of *H. atlanticus, P. maculatus* and *A. verrucosus* were of a similar size to *C. serrulatus* but their CS activities were less than one third. They were much less than that of *C. subserrulatus* even accounting for the smaller size. The CS values for the other species were between 0.1 and 0.2 except *C. crepidater*, which was less than 0.1. CS in *H. atlanticus* and *A. verrucosus* scaled significantly (Table 3, Figure 3) and the scaling coefficients were similar to the generalised scaling coefficient of -0.26 for mass-specific aerobic metabolism (Peters 1983). *Alepocephalus* sp. 1 had a $b$ coefficient of -0.31 and the *Coryphaenoides* species were both less than -0.2 but

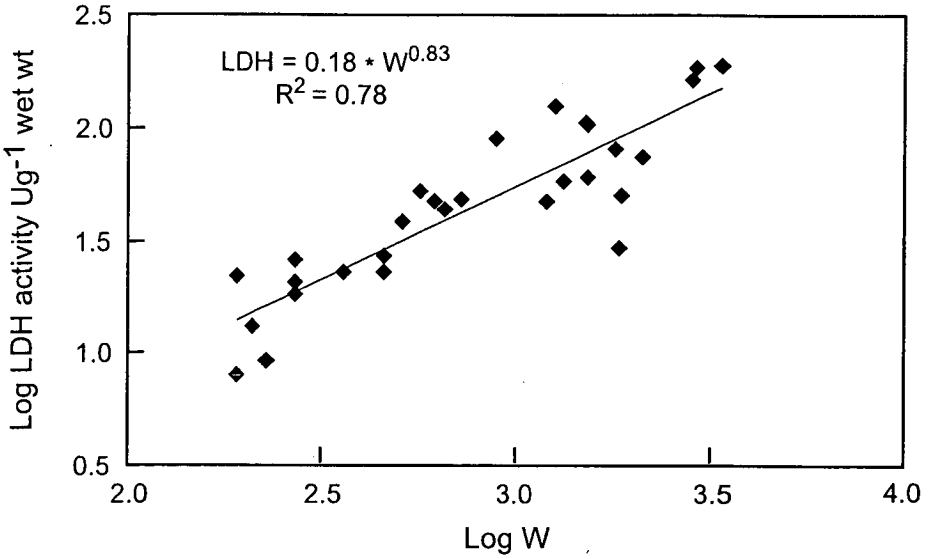


**Fig.1.** Relationship of lactate dehydrogenase (LDH) activity ($Ug^{-1}$ wet wt) with body weight (g) in orange roughy *Hoplostethus atlanticus.*

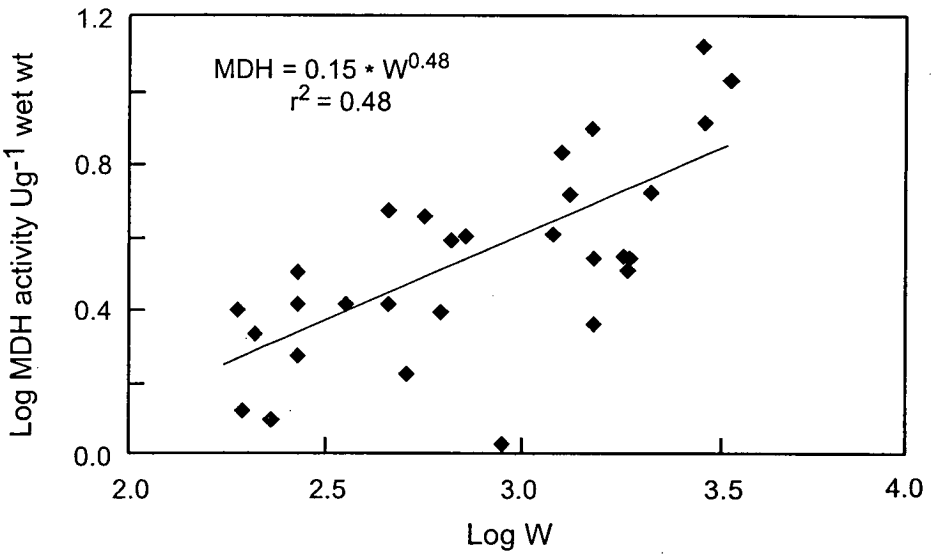


**Fig. 2.** Relationship of malate dehydrogenase (MDH) activity ($Ug^{-1}$ wet wt) with body weight (g) in orange roughy *Hoplostethus atlanticus.*

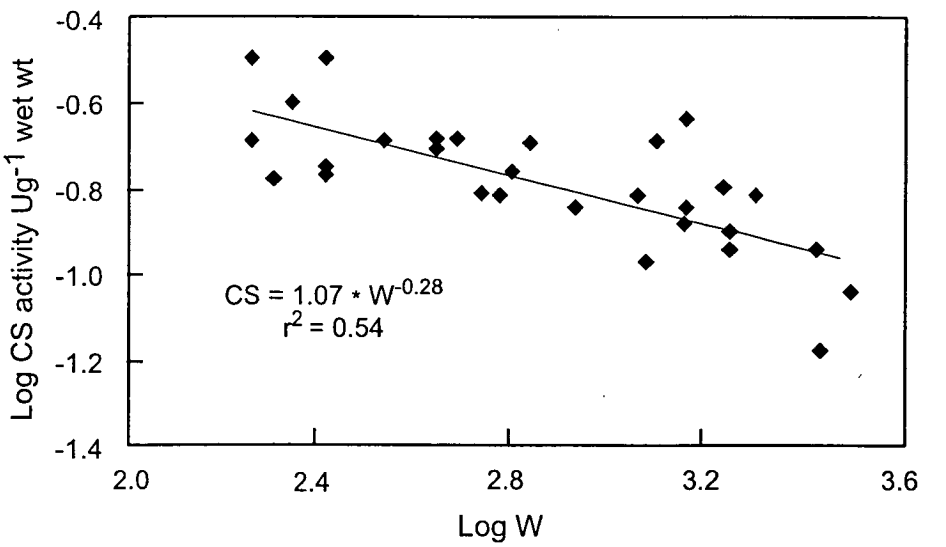


**Fig. 3.** Relationship of citrate synthase (CS) activity ($Ug^{-1}$ wet wt) with body weight (g) in orange roughy *Hoplostethus atlanticus.*

none of the relationships was significant. *P. maculatus* did not scale and *Alepocephalus* sp. 1 appeared to scale positively but was not significant.

**Table 2. Mean activities of LDH, MDH and CS, and protein and water contents of eight demersal mid-slope fishes off southern Tasmania.** Enzyme activity is expressed in international units of activity per g wet wt of white muscle, $Ug^{-1}$, at 10°C. International units of activity, U, are moles substrate converted per min. Protein is in mg $g^{-1}$ wet weight.

| Species | n | Mean wt (kg) | LDH | MDH | CS | Protein | % water |
|---|---|---|---|---|---|---|---|
| *Hoplostethus atlanticus* | 13 (ad)<br>16(juv) | 1.92±0.72<br>0.43±0.18 | 98.00±53.64<br>31.27±20.65 | 5.97±3.28<br>2.66±1.15 | 0.14±0.05<br>0.21±0.05 | 120.26 | 78.86 |
| *Pseudocyttus maculatus* | 5 (ad)<br>3 (juv) | 2.19±0.68<br>0.21±0.03 | 162.54±24.95<br>138.64±46.63 | 12.57±3.31<br>11.38±3.54 | 0.15±0.03<br>0.16±0.06 | 112.14 | 74.32 |
| *Allocyttus verrucosus* | 6 (ad)<br>11 juv | 0.68±0.16<br>0.31±0.13 | 44.37±18.49<br>22.21±16.99 | 6.84±2.19<br>5.80±1.53 | 0.18±0.05<br>0.24±0.06 | 131.43 | 78.79 |
| *Centroscymnus crepidater* | 1 | 1.75 | 108.15 | n.d. | 0.06 | n.d. | 80.00 |
| *Coryphaenoides subserrulatus* | 20 | 0.10±0.03 | 6.07±2.24 | 8.94±2.00 | 1.25±0.15 | 140.44 | 80.64 |
| *Coryphaenoides serrulatus* | 4 | 0.33±0.10 | 4.01±0.93 | 7.32±1.33 | 0.73±0.05 | 89.34 | 80.59 |
| *Alepocephalus* sp. 1 | 13 | 1.63±0.61 | 31.00±11.89 | 3.04±0.90 | 0.16±0.06 | 73.66 | 90.26 |
| *Alepocephalus* sp. 2 | 3 | 0.97±0.31 | 10.94±5.8 | 2.01±0.99 | 0.10±0.06 | 90.19 | 89.70 |

*Protein and water contents*

Protein contents of white muscle tissue ranged from 73.66 mg $g^{-1}$ in *Alepocephalus* sp. 1 to 140.44 mg $g^{-1}$ in *C. subserrulatus* (Table 2). Water contents of white muscle tissue ranged from 74.3% in *P. maculatus* to 90.3% in *Alepocephalus* sp. 1 (Table 2). *H. atlanticus*, *P. maculatus* and *A. verrucosus* had high protein concentrations ($\bar{x}$=121 mg/g) and low water contents ($\bar{x}$=77%). The protein content of *C. subserrulatus* was the highest, but that of *C. serrulatus* was

**Table 3. Regression parameters of relationships between mass-specific enzyme activity, $y^{-1}$, and weight, W for 7 demersal mid-slope fish species off southern Tasmania.** $y^{-1}=aW^b$. * indicates significance where P <5%.

| Species | n | Size range (kg) | Enzyme | a | b | ±se | F | P | $r^2$ |
|---|---|---|---|---|---|---|---|---|---|
| *Hoplostethus atlanticus* | 29 | 0.19-3.35 | LDH | 0.18 | 0.83 | 0.09 | 97.05 | 0.000* | 0.78 |
| | | | MDH | 0.15 | 0.48 | 0.09 | 25.08 | 0.000* | 0.48 |
| | | | CS | 1.07 | -0.28 | 0.05 | 31.25 | 0.000* | 0.54 |
| *Pseudocyttus maculatus* | 8 | 0.18-3.15 | LDH | 87.65 | 0.08 | 0.08 | 1.08 | 0.338 | 0.15 |
| | | | MDH | 8.26 | 0.05 | 0.09 | 0.31 | 0.596 | 0.05 |
| | | | CS | 0.16 | -0.01 | 0.08 | 0.01 | 0.918 | 0.00 |
| *Allocyttus verrucosus* | 17 | 0.08-0.89 | LDH | 0.06 | 0.99 | 0.22 | 21.19 | 0.000* | 0.59 |
| | | | MDH | 7.28 | -0.03 | 0.11 | 0.09 | 0.768 | 0.01 |
| | | | CS | 1.35 | -0.32 | 0.09 | 12.73 | 0.003* | 0.46 |
| *Coryphaenoides subserrulatus* | 20 | 0.04-0.15 | LDH | 0.19 | 0.75 | 0.18 | 17.61 | 0.001* | 0.50 |
| | | | MDH | 2.61 | 0.27 | 0.15 | 3.21 | 0.090 | 0.15 |
| | | | CS | 2.24 | -0.13 | 0.07 | 3.32 | 0.085 | 0.18 |
| *Coryphaenoides serrulatus* | 4 | 0.22-0.44 | LDH | 0.12 | 0.61 | 0.27 | 5.13 | 0.152 | 0.72 |
| | | | MDH | 4.61 | 0.08 | 0.38 | 0.04 | 0.856 | 0.02 |
| | | | CS | 2.16 | -0.19 | 0.07 | 6.53 | 0.125 | 0.77 |
| *Alepocephalus* sp. 1 | 13 | 0.61-2.34 | LDH | 6.91 | 0.20 | 0.25 | 0.64 | 0.440 | 0.06 |
| | | | MDH | 0.36 | 0.29 | 0.19 | 2.29 | 0.158 | 0.17 |
| | | | CS | 1.44 | -0.31 | 0.25 | 1.58 | 0.235 | 0.13 |
| *Alepocephalus* sp. 2 | 3 | 0.65-1.26 | LDH | 0.00 | 1.15 | 0.89 | 1.66 | 0.420 | 0.62 |
| | | | MDH | 0.03 | 0.62 | 0.72 | 0.74 | 0.547 | 0.43 |
| | | | CS | 0.00 | 0.96 | 0.88 | 1.20 | 0.471 | 0.55 |

relatively low. Both had water contents about 81%, similar to the previous three species. *C. crepidater* also had similar water content. The alepocephalids had the lowest protein contents and the highest water contents.

*Enzyme activity and oxygen consumption rate relationships*

Regressions of LDH, MDH and CS against oxygen consumption for pelagic species from the literature were significant (Figures 4-6) while only the CS

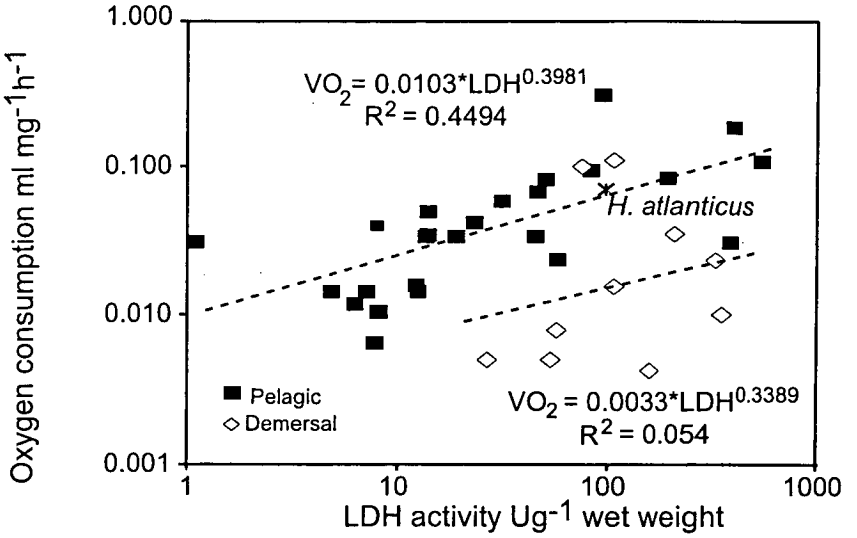


**Fig. 4.** Relationship of LDH activities and oxygen consumption rates of demersal and pelagic fishes. Pelagic species regression: P=0.0002. Demersal species regression was not significant.

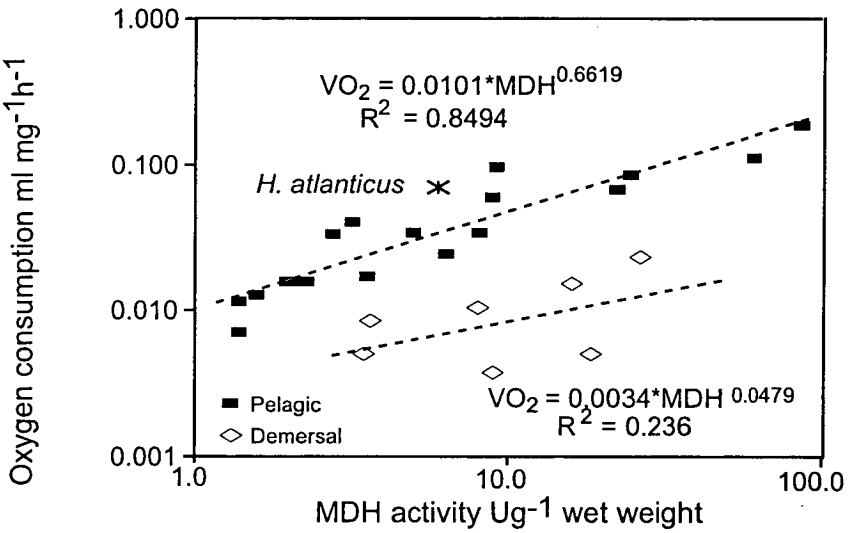


**Fig. 5.** Relationship of MDH activities and oxygen consumption rates of demersal and pelagic fishes. Pelagic species regression: P<<0.001. Demersal species regression was not significant.

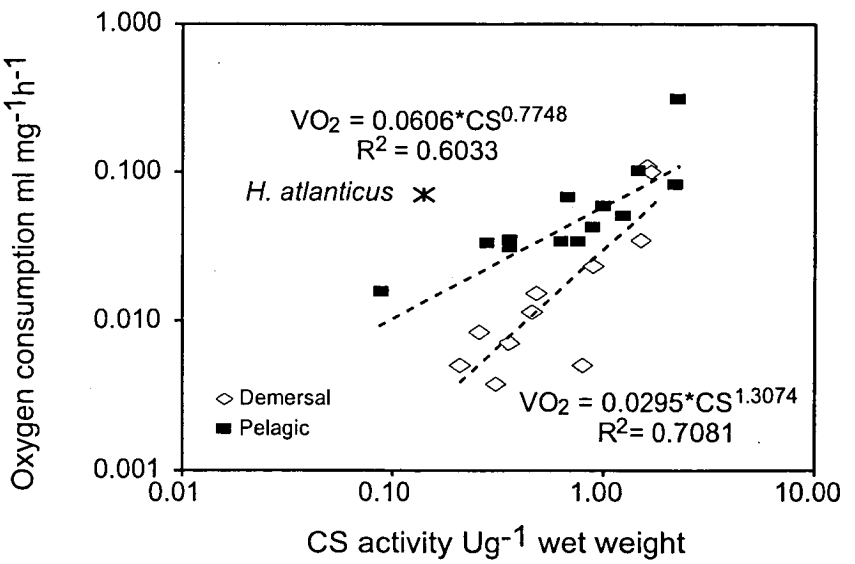


**Fig. 6.** Relationship of CS activities and oxygen consumption rates of demersal and pelagic fishes . Demersal species regression: P=0.002. Pelagic species regression: P=0.001.

regression for demersal fishes was significant (Figures 4-6). The slopes and the elevations of the CS regressions for demersal and pelagic fishes were compared to determine whether they were significantly different (Zar 1984). The slopes were not significantly different ($P$=0.13) but the elevations were ($P$=0.008), therefore the demersal fishes had higher CS activities at a given oxygen consumption rate than pelagic fishes.

**Table 4. Estimated O2 consumption rates μmol g-1 h-1 for adult Hoplostethus atlanticus using empirical relationships derived from enzyme activities, LDH, MDH and CS, and oxygen consumption rates for a variety of fish species.** Species and data listed in Table 1.

| Enzyme | Pelagic | Demersal |
|---|---|---|
| LDH | 0.0637 | 0.0155 |
| MDH | 0.0329 | 0.0069 |
| CS | 0.8279 | 0.0023 |

The oxygen consumption value for *H. atlanticus* was significantly different only from the distribution observed in the MDH against oxygen consumption regression for demersal fishes (P=0.02) although that relationship was not significant. However, it could have fitted in either of the distributions observed for the CS against oxygen consumptions for demersal fishes or pelagic fishes ($P$ =0.77 and 0.81 respectively). Estimated oxygen consumption based on food consumption was over an order of magnitude greater than that based on the demersal fishes CS relationship and about seven times greater than that based on the pelagic fishes, (0.07 cf. 0.0023 and 0.0132 respectively; Table 4). However, it was quite similar to that based on the pelagic fishes LDH relationship (0.064).

## Discussion

*Comparison of enzyme activities and scaling*

By comparing the LDH activities of the species from this study to those of other deepwater species, we can infer something of their locomotory habits. They are all anaerobically poised with LDH activities greater than their CS activities. The LDH activities of adult *Pseudocyttus maculatus*, *Centroscymnus crepidater and Hoplostethus atlanticus* are higher than the majority of deep-living species studied by Childress and Somero (1979) and Sullivan and Somero (1980) and signify relatively high activity. For instance, LDH activity of *P. maculatus* is similar to *Coryphaenoides acrolepis, C. armatus* and *Histiobranchus bathybius*, all of which are considered robust swimmers (Sullivan and Somero 1980). LDH activities of *C. crepidater* and *H. atlanticus* are very similar to the sablefish *Anoplopoma fimbria* which is also inhabits seamounts (Rogers 1994). Since *P. maculatus* and *H. atlanticus* live on seamounts and have to contend with the strong currents associated with the topography, higher levels of anaerobic metabolic activity, and consequently LDH, would be expected. LDH activity of *A. verrucosus* is intermediate. It is often found on the lower slopes of seamounts and its diet indicates bouts of active foraging.

The other species from this study are apparently less active and belong to the group of fishes that are dispersed over the sea floor. The LDH activity of *Alepocephalus* sp. 1 is similar to those of *Paraliparis rosaceus* and *Antimoro rostrata,* which have been observed drifting over the bottom in deep-water (Sullivan and Somero 1980), but being a much larger fish would imply even lower activity. LDH of *Alepocephalus* sp. 2 is similar to that of *Halosauropsis macrochir*, which has also been observed drifting over the bottom (Sullivan and Somero 1980). Many Alepocephalids are passive foragers, exhibiting a 'sit- (or drift)-and-wait' strategy, sometimes floating in unusual positions (Gartner *et al.* 1997). The very low LDH activities of the *Coryphaenoides* species are similar to those of *Coryphaenoides leptolepis,* a benthic feeder, and other deep-sea fishes that exhibit sluggish activity and a 'sit-and-wait' feeding habit.

Scaling of LDH activity can vary widely: *b* co-efficients as low as -0.7 for larval *Brevoortia tyrannus* (Power and Walsh 1992) and as high as 1.025 for *Gymnoscopelus opisthopterus* (Torres and Somero 1988b) have been measured. Somero and Childress (1985) suggested the highest scaling of LDH activity occurred in the strongest swimmers, such as the subcarangiforms, which rely on burst locomotion for predation and predator avoidance. They proposed that increased glycolytic enzyme activity in white muscle is responsible for the increase in anaerobic power in larger fishes (Somero and Childress 1990). Based on their conclusions, the LDH scaling co-efficients for *H. atlanticus*, *A. verrucosus* and the *C. subserrulatus* support the notion that these species are active swimmers, at least over the size range measured.

Scaling characteristics of anaerobic enzyme activities also reflect ontogenetic changes in lifestyle. Scaling co-efficients can actually change sign during life-history, e.g., scaling of LDH in *Sebastolobus altivelis* larvae changes throughout early life (Siebenaller 1984) and juvenile *S. alascanus* have been shown to scale differently to adults (Vetter and Lynn 1997). Juvenile *H. atlanticus* are associated with the bottom (Mace *et al.* 1990, Bulman and Elliott 1994) and are probably much less energetic than the benthopelagic adults particularly those from the seamounts. LDH in *P. maculatus* did not scale. Vetter and Lynn (1997) found a similar situation in *S. alascanus,* where LDH did not appear to scale overall but separately, juveniles scaled positively and adults negatively, reflecting their ontogenetic migration into deeper water. Small juveniles of *P. maculatus* are pelagic for 5–6 years (James *et al.* 1988, Annala 1995), after which they migrate into deeper water. Although nothing is known of the enzyme levels or scaling at this size, lack of LDH scaling in larger juveniles and adults supports the notion of an ontogenetic reduction in activity. On the other hand, *A. verrucosus* has a similar but shorter pelagic phase of 4–5 years (Stewart *et al.* 1995) but LDH does scale, although not as strongly as *H. atlanticus*. *A. verrucosus* eats pelagic crustaceans, fish and squid, prey similar to those of *H. atlanticus,* that require at least a moderate amount of activity to capture, whereas *P. maculatus* eats mostly pyrosomes that require less energy to capture and are lower in calories (Blaber and Bulman 1986). Therefore, differences in feeding strategies might also be contributing to the expression of enzyme activities in these species.

MDH activities of the species studied here showed a similar, but less pronounced, association with activity patterns to that of LDH activities. MDH activity of *P. maculatus* was similar to those of the more active deep-sea species (Sullivan and Somero 1980) and several of the shallow-water pelagic species (Childress and Somero 1979). MDH activity of *H. atlanticus* was similar to activities of the less active deep-water species but higher than many pelagic deep-water species (Childress and Somero 1979). *Coryphaenoides* species' activities were similar to those of the less active deepwater macrourids such as *C. carapinus*, *C. rupestris* and *C. leptolepis* (Siebenaller *et al.* 1982). MDH is possibly higher in active fish because of its importance in the redox balance during burst activity (Sullivan and Somero 1980).

A wide range of MDH scaling coefficients is found amongst other fishes: from -0.32 for *S. altivelis* (Vetter and Lynn 1997) up to 1.21 in *Scorpaena guttata* (Yang and Somero 1993). Only *H. atlanticus* scaled significantly for MDH, $b$=0.48, which in view of its likely role in redox, corroborates the active lifestyle expected from LDH findings.

The activities of CS of the two *Coryphaenoides* species were relatively high but generally, CS varied little between the other species. A similar lack of variation was reported amongst the species studied by Sullivan and Somero (1980) and they concluded that this was because white muscle does not carry on much aerobic activity and most differences were depth-related. Somero and Childress (1980) reported negative scaling coefficients of CS activities such that small individuals have higher CS levels. The *Coryphaenoides* species were the smallest species we studied but, their CS activities were slightly, to much, higher than activities of other macrourids from a similar depth range (Siebenaller *et al.* 1982). Even by scaling the CS activity of *C. subserrulatus* up to 300g, the average weight of *C. armatus,* it was higher than that of *C. armatus* (1.07 $Ug^{-1}$ ±0.214 (SE) *c.f.* 0.79 $Ug^{-1}$). CS in *H. atlanticus* and *A. verrucosus* both scaled significantly and the values were similar to the mass-specific scaling factor for metabolism of -0.25.

Thuesen *et al.* (1998) showed that among copepods the ratio of LDH to CS activity was distinct for each species and that it reflected morphology and behaviour. For a group of fishes occurring at depths greater than 200m including those from this

study (Childress and Thuesen 1995, Siebenaller *et al.* 1982, Sullivan and Somero 1980, Torres and Somero 1988b, Vetter and Lynn 1997, Vetter *et al.* 1994, Yang and Somero 1993), LDH and CS activities were plotted on a log-log scale (Fig. 7). The ratio of the glycolytic potential to aerobic metabolism for individual species also supports their specific morphological, behavioural and ontogenetic characteristics. The macrourids generally had relatively high CS activities and low LDH activities, reflecting a slowly cruising predatory habit but with varying levels of burst activity. Another group, with CS values an order of magnitude lower but a slightly higher range of LDH activities, included the benthic species, *Sebastolobus* species and benthopelagic species *Alepocephalus* sp. 1 and *A. verrucosus* from this study. *H. atlanticus*, *P. maculatus* and the flatfishes appeared to form a group of relatively high LDH activities but low CS activities. The latter species either did not scale or scaled negatively, reflecting ontogenetic changes from more active juvenile phases to less active, benthic adult phase. They were sit-and-wait predators. *H. atlanticus* scaled positively for LDH (this study), indicating the species is relatively more active. However *Histiobranchus bathybius*, *C. acrolepis, A. fimbria,* and *B. hollisi*, a fish found around hydrothermal vents, had higher CS activities than the benthic group but a similar range of LDH activities. *Trematomus loenbergii* and *Rhigophila dearborni*, Antarctic benthic fishes, had quite high CS and LDH activities, placing them quite apart. *C. armatus* was placed on its own, midway between the last group and the macrourids. Similar patterns could be seen in a comparison in Koslow (1997) although only about half the species were the same.

*Proximate composition*

Generally, water increases and protein decreases with depth in fishes (Childress and Nygaard 1973, Torres *et al.* 1979, Somero *et al.* 1983, Crabtree 1995). A decrease in protein with depth in fish (and midwater crustaceans) is presumed to be a limiting factor to locomotory capacity (Childress 1995) and consequently metabolism. Furthermore, skeletal muscle constitutes ~70% of total body mass, therefore any reduction in muscle mass would be expected to reduce metabolic cost considerably (Gibbs 1997). Therefore, relatively active deep-living fish would be expected to have correspondingly higher muscle mass, protein content and metabolic

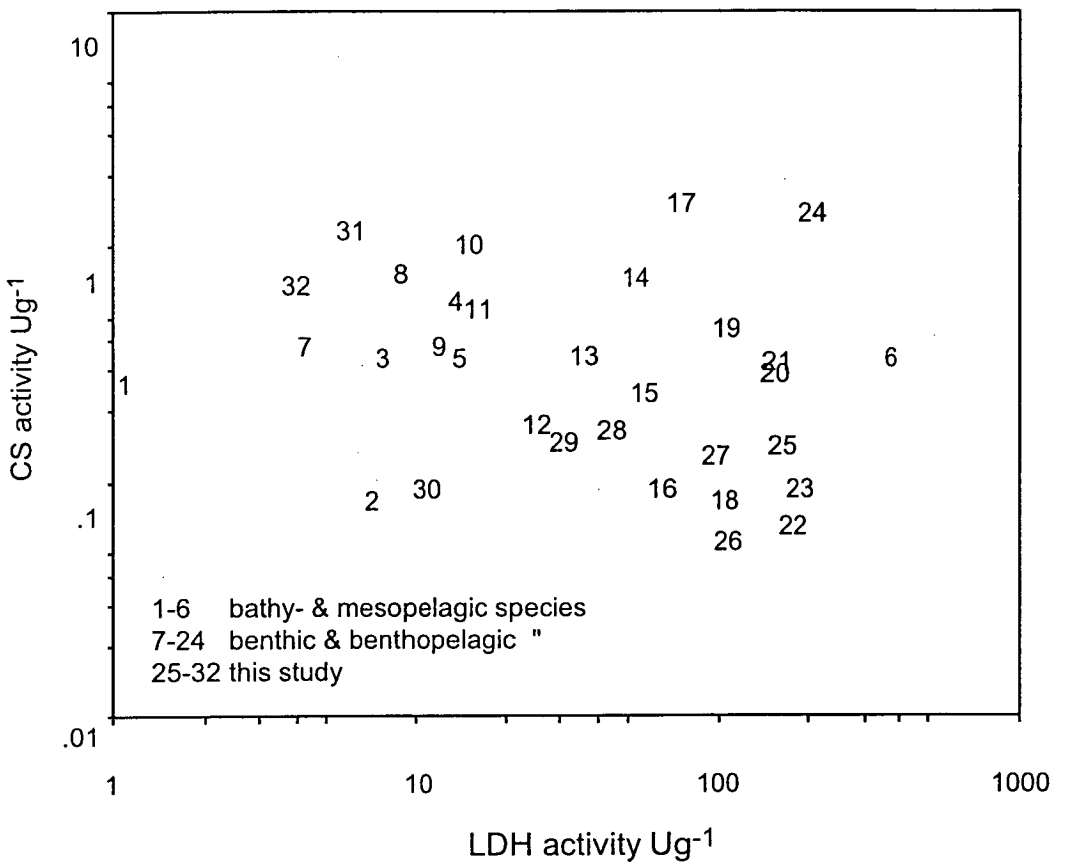


**Fig.7.** Mean LDH and mean CS activities for fishes. Data from: Childress and Thuesen 1995, Siebenaller et al. 1982, Sullivan and Somero 1980, Torres and Somero 1988b, Vetter and Lynn 1997, Vetter et al. 1994 and Yang and Somero 1993 and this study. Species are: 1 *Borostomias panamensis,* 2 *Bathylagus milleri,* 3 *Bajacalifornia burragei,* 4 *Cyclothone acclinidens,* 5 *Bathylagus antarcticus,* 6 *Cyclothone microdon,* 7 *Coryphaenoides leptolepis,* 8 *Nezumia bairdii,* 9 *Halosauropsis macrochir,* 10 *Coryphaenoides carapinus,* 11 *Coryphaenoides rupestris,* 12 *Sebastolobus altivelis,* 13 *Antimoro rostrata,* 14 *Coryphaenoides armatus,* 15 *Sebastolobus alascanus,* 16 *Paraliparis rosaceus,* 17 *Trematomus loenbergii,* 18 *Glyptocephalus zachirus,* 19 *Anoplopoma fimbria,* 20 *Coryphaenoides acrolepis,* 21 *Histiobranchus bathybius,* 22 *Embassichthys bathybius,* 23 *Microstomus pacificus,* 24 *Rhigophila dearborni,* 25 *Pseudocyttus maculatus,* 26 *Centroscymnus crepidater,* 27 *Hoplostethus atlanticus,* 28 *Allocyttus verrucosus,* 29 *Alepocephalus* sp. 1, 30 *Alepocephalus* sp. 2, 31 *Coryphaenoides subserrulatus,* 32 *Coryphaenoides serrulatus.*

costs. Crabtree (1995) studied the chemical composition of 48 demersal species and found that the group of benthopelagic species possessing swimbladders had a mean water content of 80% and a mean protein content of 13% wet weight (assuming average nitrogen content of protein to be 16% (Houk and Ue 1974). The seamount fishes, *H. atlanticus* and *P. maculatus*, and the benthopelagic fishes, *A. verrucosus*, *C. subserrulatus* and *C. crepidater* had similar water and protein contents. One of the metabolic costs of possessing a dense bodily composition is maintaining neutral buoyancy, usually overcome by a swim bladder.

The possession of a swim bladder in itself influences proximate composition. To maintain neutral buoyancy by more dilute body fluids, benthopelagic fishes without swimbladders have higher water content and lower carbon (=lipid), nitrogen (=protein) and energy content than benthopelagic species with swimbladders or benthic species (Crabtree 1995). The same appears to be true for midwater species, with and without swimbladders (Childress and Nygaard 1973). Water contents of the two Alepocephalids in this study, which do not possess swimbladders, were similar to those of benthopelagic fishes without swim bladders and very similar to Alepocephalids found by Crabtree (1995). He suggested that species in this particular group are energetically very efficient because of their low-density body fluids.

In contrast, *H. atlanticus* possesses a lipid-filled swimbladder and the squalid *C. crepidater* possesses a large oily liver both of which may be energetically expensive to maintain. However, this expense is offset by their enhanced ability to swim and capture food despite their dense body. The lipid content of the flesh of roughy can vary from 3-10% (Bakes *et al.* 1997, Buisson *et al.* 1982) probably due to nutritional and reproductive status of the fish. However, only one study has determined total lipid of the whole body –18%(Buisson *et al.* 1982)–and over 40% of it is found in the head (similarly for oreos). An Antarctic Notothenid, *Pleuragramma antarcticum*, also uses lipid sacs as a buoyancy mechanism in addition to a relatively reduced skeletal ossification (De Vries and Eastman 1978). However, as ossification of the head increases with age so does the lipid content of the fish. The roughy also has reduced skeletal ossification compared to other deepwater species of comparable size and this, in combination with a high total lipid content, enables it to maintain neutral buoyancy despite its relatively high protein content.

Both oreos have gas-filled swim bladders although it is less pronounced in *P. maculatus* (R. Kloser, pers. comm.). *A. verrucosus* is able to maintain neutral buoyancy with higher levels of lipid in muscle, offsetting higher protein contents, and a well-developed swim bladder. However, compared to *Allocyttus* sp. and *H. atlanticus*, the lipid content of *P. maculatus* is low (~6% c.f.~15% and~18%)(Buisson *et al.* 1982, Phleger 1991), as are water and protein contents. Therefore, the less dense bodily composition and a reduced swim bladder must adequately compensate negative buoyancy effects.

*Coryphaenoides subserrulatus* has an unusual swimbladder that appears to be a spongy matrix whereas *C. serrulatus* has an ordinary gas-filled bladder (M. Lewis, CSIRO pers. comm.). Fat-invested swimbladders are fairly common in deep water *Coryphaenoides* (Phleger 1991) enabling them to maintain neutral buoyancy fundamental to their slow-cruising but posturally versatile lifestyle (Marshall 1979). The apparently higher lipid content of the swimbladder of *C. subserrulatus* would offset its higher muscle protein not necessary for *C. serrulatus*.

*Comparison of oxygen consumption estimates for H. atlanticus*

The disparity between the oxygen consumption estimates for *H. atlanticus* based on the three enzymes and the original estimate is puzzling. *H. atlanticus* metabolism appears to be greater than the rates of most deep-sea benthic or benthopelagic species (Bulman and Koslow 1992, Table 3). It is noted as being an active species (Koslow *et al.* 1995, Koslow 1996) but relaxed selection for locomotion due to reduced light has been strongly argued as a major factor affecting metabolism (Childress 1995). Much of what we know of its habits indicate this: around a seamount, *H. atlanticus* gains and maintains position in the strong current patterns; it forages in the water column for pelagic prey such as prawns, midwater fishes and squid (Bulman and Koslow 1992); it migrates to the east coast of Tasmania to spawn, a distance of some hundreds of kilometres (although Jobling (1994) suggests that migrations could be less costly than expected); it is difficult to capture when trawling through schools off the bottom and is often caught by 'chasing' fish down hills (Koslow 1996); and it is easily frightened when camera systems are lowered into schools (Koslow *et al.* 1995). Confirming our own

inferences, Lorance (2001) observed orange roughy from a submersible, exhibiting behaviour ranging from highly active to inactive, where they were observed resting on the bottom in areas with no currents.

Despite the evidence to indicate an active lifestyle and the high metabolic rate estimated from the bioenergetic model, the mean enzyme activities of *H. atlanticus* are not greatly distinguishable from other similarly sized benthopelagic fishes including other seamount fishes. However, the relationships between enzyme activities and oxygen consumption rates derived from the few data for benthic and benthopelagic fishes were inadequate to estimate oxygen consumption of *H. atlanticus* from enzyme activities. Thuesen *et al.* 1998 were also unable to estimate oxygen consumption rates for copepods using CS activities.

Factors that might influence metabolic rates were recently reviewed by Gibbs (1997) but do not explain the apparent disparity. For instance, LDH is quite 'plastic' in expression and nutritional status has been shown to affect LDH activity (Sullivan and Somero 1983, Yang and Somero 1993, Vetter *et al.* 1994, Gibbs 1997, Vetter and Lynn 1997) and proximate composition. Experiments on Dover Sole *Microstomus pacificus* showed that when rations were increased, LDH also increased (Vetter *et al.* 1994). Vetter and Lynn (1997) concluded that increases in LDH, MDH and CS in *Sebastolobus altivelis* were also probably due to increased food resources. Conversely, starved *Sebastolobus* sp. had reduced levels of LDH, similar to those of wild fish (Yang and Somero 1993) and similar reductions were found in *Anoplopoma fimbria* (Sullivan and Somero 1983). Increased rations also result in higher lipid stores and caloric density and consequently higher metabolism. The seamount fishes appear to have good access to food resources. Orange roughy consumes about 1% body weight per day similar to mesopelagic migrators (Bulman and Koslow 1992), six times higher than for other dispersed demersal fishes (Koslow 1996). Proximate compositions and enzyme activities also suggest good food availability but not enough to account for the estimated metabolic rate of *H. atlanticus*.

If we assume the field estimate of oxygen consumption for *H. atlanticus* was nearly right, then the LDH relationship derived for pelagic fishes produced the best estimate of oxygen consumption. Although the oxygen consumption estimate was not statistically different from either of the CS relationship distributions it was

higher than both. Using the pelagic LDH relationship, *P. maculatus* and *A. verrucosus* would have oxygen consumptions rates of 0.08 and 0.05 $\mu l\ mg^{-1}\ h^{-1}$. Those estimates place them somewhat higher than expected from CS relationships, similar to *H. atlanticus*. A new relationship between CS activity and oxygen consumption for roughy and the group of seamount-associated fishes might be required, perhaps with a greater elevation. This might be because the oxygen debt accumulated during anaerobic bursts of activity paid back during periods of quiescence, increases overall metabolism to such a degree that it cannot be estimated by the current CS activity relationships.

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## References


**Annala, J.H.** (ed.) (1995). Report from the Fishery Assessment Plenary, May 1995: Stock assessments and yield estimates. Unpublished report. New Zealand (Ministry of Agriculture and Fisheries, New Zealand.) 277 pp.

**Bakes, M.J., Elliott, N.J., Green, G.J. and Nicholls, P.D.** (1995). Variation in lipid composition of some deep-sea fish (Teleostei: Oreosomatidae and Trachichthyidae). *Comparative Biochemistry and Physiology* **111B**: 633-642.

**Blaber, S.J.M., and Bulman C.M.** (1987). Diets of fishes of the upper continental slope of eastern Tasmania: content, calorific values, dietary overlap and trophic relationships. *Marine Biology* **95**: 345-356.

**Bulman, C.M. and Elliott, N.G.** (1994). 1987 Orange roughy exploratory cruises off Tasmania. *CSIRO Marine Laboratories Report* **214**. 49 pp.

**Bulman, C.M. and Koslow, J.A.** (1992). Diet and food consumption of a deep-sea fish, orange roughy *H. atlanticus* (Pisces: Trachichthyidae), off southeastern Australia. *Marine Ecology Progress Series* **82**: 115-129.

**Bulman, C.M., He, X. and Koslow, J.A.** (2002). Trophic ecology of the mid-slope demersal fish community off southern Tasmania, Australia. *Marine and Freshwater Research 53*: 59-72.

**Buisson, D.H., Body, D.R, Dougherty, G.J., Eyres, L. and Vlieg, P.** (1982). Oil from deep water fish species as a substitute for sperm whale and jojoba oils. *Journal of American Oil Chemistry Society* **59**: 390-395.

**Childress, J.J.** (1995). Are there physiological and biochemical adaptations of metabolism in deep-sea animals? *Trends in Ecology and Evolution* **10**: 30-36.

**Childress, J.J., Cowles, D.L., Favuzzi, J.A., and Mickel, T.J.** (1990). Metabolic rates of benthic deep-sea decapod crustaceans decline with increasing depth primarily due to the decline in temperature. *Deep-Sea Research* **37**: 929-949.

**Childress, J.J. and Mickel, T. J.** (1985). Metabolic rates of animals from the hydrothermal vents and other deep-sea habitats. *Bulletin of the Biological Society (Washington)* **6**: 249-260.

**Childress, J.J. and Nygaard, M.H.** (1973). The chemical composition of midwater fishes as a function of depth of occurrence off southern California. *Deep-Sea Research* **20**: 1093-1109.

**Childress, J.J. and Somero, G.N.** (1979). Depth-related enzymic activities in muscle, brain and heart of deep-living pelagic marine teleosts. *Marine Biology* **52**: 273-283.

**Childress, J.J. and Somero, G.N.** (1990). Metabolic scaling: a new perspective based on scaling of glycolytic enzyme activities. *American Zoologist* **30**: 161-173.

**Childress, J.J. and Theusen, E.V.** (1992). Metabolic potential of deep-sea animals: regional and global scales. pp. 217-236. *In*: G. T. Rowe and Pariente, V. (eds). 'Food Chains and Global Carbon Cycles'. (Kluwer Academic Publishers, Dordrecht.)

**Childress, J.J. and E.V. Theusen**. 1995. Metabolic potentials of deep-sea fishes: A comparative approach. pp.175-196. *In:* P.W. Hochachka and Mommsen, T.P. (eds). 'Biochemistry and Molecular Biology of Fishes Vol. 5.' (Elsevier, Amsterdam.)

**Charuau, A., Dupouy, H. Lorance, and P.** (1995). French exploitation of the deepwater fisheries of the North Atlantic. pp.337-356. *In*: A.G. Hopper (ed.). 'Deep-water Fisheries of the North Atlantic Oceanic Slope.' Kluwer Academic Publishers, Dordrecht.)

**Cowles, D.L., Childress, J.J. and Wells, M.E.** (1991). Metabolic rates of midwater crustaceans as a function of depth of occurrence off the Hawaiian Islands: food availability as a selective factor? *Marine Biology* **110**: 75-83.

**Crabtree, R.E.** (1995). Chemical composition and energy content of deep-sea demersal fishes from tropical and temperate regions of the western North Atlantic. *Bulletin of Marine Science* **56**: 434-449.

**Crabtree, B. and Newsholme, E.A.** (1972). The activities of phosphorylase, hexokinase, phosphofructokinase, lactate dehydrogenase and glycerol 3-phosphate dehydrogenases in muscles from vertebrates and invertebrates. *Biochemical Journal* **126**: 49-58.

**De Vries, A. L. and Eastman, J.T.** (1978). Lipid sacs as a buoyancy adaptation in an Antarctic fish. *Nature* **271**: 352-353.

**Gartner, J.V., Jr, Crabtree, R.E. and Sulak, K.J.** (1997). Feeding at depth. pp. 115-193. *In:* D.J. Randall and A.P. Farrell (eds). 'Deep Sea Fishes'. (Academic Press, San Diego.)

**Gibbs, A.G.** (1997). Biochemistry at depth. pp. 239-277. *In:* D.J. Randall and A.P. Farrell (eds). 'Deep Sea Fishes'. (Academic Press, San Diego.)

**Houk , T.W. and Ue, K.** (1974). The measurement of actin concentration in solution: a comparison of methods. *Analytical Biochemistry* **62**: 66-74.

**Hochachka, P.W. and Somero, G.N.** (1984). 'Biochemical Adaptation.' (Princeton University Press, Princeton, N. J.) 537 pp.

**James, G.D., Inada, T. and Nakamura, I.** (1988). Revision of the oreosomatid fishes (Family Oreosomatidae) from the southern oceans, with a description of a new species. *New Zealand Journal of Zoology* **15**: 291-326.

**Jobling, M.** (1994). 'Fish Bioenergetics.' (Chapman and Hall, London.) 309 pp.

**Koslow, J.A.** (1996). Energetic and life-history patterns of deep-sea benthic, benthopelagic and seamount-associated fish. *Journal of Fish Biology* **49A**: 54-74.

**Koslow, J.A.** (1997). Seamounts and the ecology of deep-sea fisheries. *American Scientist* **85**: 168-176.

**Koslow, J.A., Bulman, C.M. and Lyle, J.M.** (1994). The mid-slope demersal fish community off southeastern Australia. *Deep-Sea Research* **41**: 113-141.

**Koslow, J.A., Kloser, R. and Stanley, C.A.** (1995). Avoidance of a camera system by a deepwater fish, the orange roughy (*Hoplostethus atlanticus*). *Deep-Sea Research* **42**: 233-244.

**Lorance, P., Uiblein, F. and Latrouite, D.** in press. Habitat characteristics, behaviour and colour patterns of orange roughy (*Hoplostethus atlanticus*) on the bay of Biscay continental slope (NE Atlantic). *Journal of the Marine Biological Association (UK).*

**Mace, P.M., Fenaughty, J.M., Coburn, R.P. and Doonan, I.J.** (1990). Growth and productivity of orange roughy (*Hoplostethus atlanticus*) on the north Chatham Rise. *New Zealand Journal of Marine and Freshwater Research* **24**: 105-119.

**Marshall, N.B.** (1979). 'Developments in Deep-Sea Biology.' (Blandford Press, Poole, UK.) 566 pp.

**Merrett, N.R. and Haedrich, R.L** (1997). 'Deep-sea Demersal Fish and Fisheries.' (Chapman and Hall, London.) 282 pp.

**Minitab Reference Manual** 1996. (Minitab Inc, USA.)

**Peters, RH.** (1983). 'The Ecological Implications of Body Size.' (Cambridge University Press, Cambridge.) 329 pp.

**Phleger, C.F.** (1991). Biochemical aspects of buoyancy in fishes. pp. 209-247. *In:* P.W. Hochachka and T.P. Mommsen (eds). 'Biochemistry and Molecular Biology of Fishes Vol. 1.' (Elsevier, Amsterdam.)

**Power, J.H. and Walsh, P.J.** (19920. Metabolic scaling, buoyancy, and growth in larval Atlantic menhaden, *Brevoortia tyrannus. Marine Biology* **112**: 17-22.

**Rogers, A.D.** (1994). The biology of seamounts. *Advances in Marine Biology* **30**: 305-350.

**Siebenaller, J.F.** (1984). Analysis of the biochemical consequences of ontogenetic vertical migration in a deep-living teleost fish. *Physiological Zoology* **57**: 598-608.

**Siebenaller, J.F., Somero, G.N. and Haedrich, R.L.** (1982). Biochemical characteristics of macrourid fishes differing in their depths of distribution. *Biological Bulletin* **163**: 240-249.

**Schmidt-Nielsen, K.** (1979). 'Animal Physiology: Adaptation and environment.' (Cambridge University Press, Cambridge.)

**Smith, K.L.** (1978). Metabolism of the abyssopelagic rattail *Coryphaenoides armatus* measured in situ. *Nature* **274**: 362-364.

**Smith, K.L. and Brown, N.O.** (1983). Oxygen consumption of pelagic juveniles and demersal adults of the deep-sea fish *Sebastolobus altivelis*, measured at depth. *Marine Biology* **76**: 325-332.

**Smith, K.L. and Hessler, R.R.** (1974). Respiration of benthopelagic fishes: in situ measurements at 1230 meters. *Science* **184**: 72-73.

**Smith, K.L. and Laver, M.B.** (1981). Respiration of the bathypelagic fish *Cyclothone acclinidens*. *Marine Biology* **61**: 261-266.

**Somero, G.N., Anderson, A.E. and Childress, J.J.** (1989). Transport, metabolism, and detoxification of hydrogen sulfide in animals from sulfide-rich marine environments. *CRC Critical Reviews in Aquatic Science* **1**: 591-614.

**Somero, G.N. and Childress, J.J.** (1980). A violation of the metabolism-size scaling paradigm: activities of glycolytic enzymes in muscle increase in larger-size fish. *Physiological Zoology* **53**: 322-337.

**Somero, G.N. and Childress, J.J.** (1985). Scaling of oxidative and glycolytic enzyme activities in fish muscle. pp. 250-262. *In:* R. Gilles (ed.). 'Circulation, Respiration and Metabolism,' (Springer-Verlag, Berlin.)

**Somero, G.N. and Childress, J.J.** (1990). Scaling of ATP-supplying enzymes, myofibrillar proteins and buffering capacity in fish muscle: relationship to locomotory habit. *Journal of Experimental Biology* **149**: 319-333.

**Somero, G.N., Siebenaller, J.F. and Hochachka, P.W.** (1983). Biochemical and physiological adaptations of deep-sea animals. pp. 261-330. *In:* G. T. Rowe (ed.).' The Sea Vol. 8,' (Wiley, New York.)

**Stewart, B.D., Fenton, G.E., Smith, D.C. and Short, S.A.** (1995). Validation of otolith-increment age estimates for a deepwater fish species, the warty dory, *Allocyttus verrucosus*, by radiometric analysis. *Marine Biology* **123**: 29-38.

**Sullivan, K.M. and Somero, G.N.** (1980). Enzyme activities of fish skeletal muscle and brain as influenced by depth of occurrences and habits of feeding and locomotion. *Marine Biology* **60**: 91-99.

**Sullivan, K.M. and Somero, G.N.** (1983). Size- and diet-related variation in enzymic activity and tissue composition in the sablefish, *Anoplopoma fimbria*. *Biological Bulletin* **164**: 315-326.

**Thuesen, E.V. and Childress, J.J.** (1993). Enzymatic activities and metabolic rates of pelagic chaetognaths: lack of depth-related declines. *Limnology and Oceanology* **38**: 935-948.

**Thuesen, E.V., Miller, C.B. and Childress, J.J.** (1998). Ecophysiological interpretation of oxygen consumption rates and enzymatic activities of deep-sea copepods. *Marine Ecology Progress Series* **168**: 95-107.

**Torres, J.J., Belman, B.W. and Childress, J.J.** (1979). Oxygen consumption rates of midwater fishes as a function of depth of occurrence. *Deep-Sea Res*earch **26A**: 185-197.

**Torres, J.J. and Somero, G.N.** (1988a). Vertical distribution and metabolism in Antarctic mesopelagic fishes. *Comparative Biochemistry and Physiology* **90B**: 521-528.

**Torres, J.J. and Somero, G.N.** (1988b). Metabolism, enzymic activities and cold adaptation in Antarctic mesopelagic fishes. *Marine Biology* **98**: 169-180.

**Troyanovsky, F.M. and Lisovsky, S.F.** (1995). Russian (USSR) fisheries research in deepwaters (below 500m) in the North Atlantic. pp.357-365. *In:* A.G. Hopper (ed.). 'Deep-water Fisheries of the North Atlantic Oceanic Slope.' (Kluwer Academic Publishers: Dordrecht.)

**Vetter, R.D. and Lynn, E.A.** (1997). Bathymetric demography, enzyme activity patterns, and bioenergetics of deep-living scorpaenid fishes (genera *Sebastes*

and *Sebastolobus*): paradigms revisited. *Marine Ecology Progress Series* **155**: 173-188.

**Vetter, R.D., Lynn, E.A. , Garza, M. and Costa, A.S.** (1994). Depth zonation and metabolic adaptation in Dover sole, *Microstomus pacificus*, and other deep-living flatfishes: factors that affect the sole. *Marine Biology* **120**:14-159.

**Vlieg, P.** (1983). Transmission oil from fish? *Catch* **10**: 21-22.

**Yang, T-H. and Somero, G.N.** (1993). Effects of feeding and food deprivation on oxygen consumption, muscle protein concentration and activities of energy metabolism in muscle and brain of shallow-living (*Scorpaena guttata*) and deep-living (*Sebastolobus alascanus*) Scorpaenid fishes. *Journal of Experimental Biology* **181**: 213-232.

**Zar, J. H.** (1984). 'Biostatistical Analysis.' (Prentice-Hall, New Jersey.) 718 pp.

# CHAPTER 5

## Modelling trophic interactions of the mid-slope demersal fish community off southern Tasmania, Australia

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# Modelling trophic interactions of the mid-slope demersal fish community off southern Tasmania, Australia

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**Abstract.** Ecopath with Ecosim models were developed for the demersal fish community on the flat ground of the mid-slope, and the seamounts, off southern Tasmania. This community is dominated by orange roughy *Hoplostethus atlanticus* (Trachichthyidae), several species of oreosomatids, macrourids, squalids, alepocephalids and a synaphobranchid eel. Major prey for these species includes small benthic and mesopelagic fishes, squid, pyrosomes, and pelagic crustaceans. Consumption of orange roughy and of its prey dominated the trophic structure. Trophic levels ranged from 3.0 for pyrosome-feeders to 4.9 for piscivores and the overall average for the community was 3.7. The model estimated that the amount of standing biomass of the major prey required to sustain the orange roughy biomass on the seamounts was greater than observed from field studies. Thus, it supported previous suggestions that significant energy inputs, mostly through advection, are required to sustain this community. Energy inputs of the pelagic organisms most likely to be advected, referred to as migration rates in the model, were estimated. Fishing rates on orange roughy and oreos were high in the early 1990s but their abundance decreased dramatically within a few years and rates have been low ever. These fishing rates were estimated from fishery data. Five rates of migration, along with estimated fishing rates, were set up as scenarios in the Ecosim simulations to examine potential recovery time of the fish community to the pre-fishing state. The simulation indicated that even with no further fishing on roughy, it would recover to 99% of pre-fishing biomass over the next 40 years. The oreo population was severely impacted by fishing and would recover to only 57% of pre-fishing biomass over the following 40 years. These recovery rates largely depended on advection rates. High advection rates would allow recovery of

orange roughy in less than 20 years and oreos in about 55 years while low advection rates would allow recovery to only two-thirds pre-fishing biomass for both fisheries.

## Introduction

Around seamounts on the mid-slope (700-1200 m) off southern and eastern Tasmania, Australia, orange roughy *Hoplostethus atlanticus* (Trachichthyidae) has been fished heavily since 1990. This species is dominant on flat ground also but it has been estimated that over 90% of the biomass occurs on the seamounts (Koslow *et al.* 1994). A preliminary model developed by Koslow (1997) to assess energy flow through the water column off southern Tasmania, concluded that the biomass of fish dispersed over the relatively flat parts of the seafloor could be supported by the productivity of the overlying water column. However, the aggregating species on the seamounts, including *H. atlanticus*, must be sustained by an additional input of resources. In a number of ecosystems around the world involving seamount and deep-water communities, it has been suggested that sufficient energy to sustain those communities is derived from the lateral advection of organisms past the seamounts or by impingement of organisms onto the slope from adjacent oceanic systems (Isaacs and Schwartzlose 1965, Tseitlin 1985, Pereyra *et al.* 1969, Genin *et al.* 1988).

Of primary interest was how much production was required to sustain the orange roughy stock in particular, and the demersal community more broadly, on both the flat ground and seamounts, prior to commercial fishing and during the decade of intense fishing which followed its discovery. The flat-ground and seamount demersal fish communities were modelled using Ecopath with Ecosim (EwE) ecological software.

In the1980s the mass-balance modelling approach was widely used to describe trophic structure of aquatic and terrestrial ecosystems (e.g. Polovina 1984). This approach was the basis of the Ecopath model (Christensen and Pauly 1992). Ecopath has since been evolving to incorporate features that are more relevant to dynamic situations, particularly with fisheries management in mind. The result is a suite of programs, beginning with the Ecopath model, which describes the average state of the system. This serves to parameterise the coupled difference and differential equations of Ecosim and Ecospace, which simulate temporal and spatial changes, respectively, in the

ecosystem (Pauly *et al.* 2000, Walters *et al.* 1997, 2000). Although there are limitations to these models in terms of modelling trophic flows related to age-structure (Pauly *et al.* 2000), they do provide a useful tool to utilise a wealth of knowledge of the ecosystem and the species and to explore the response of the whole ecosystem to change.

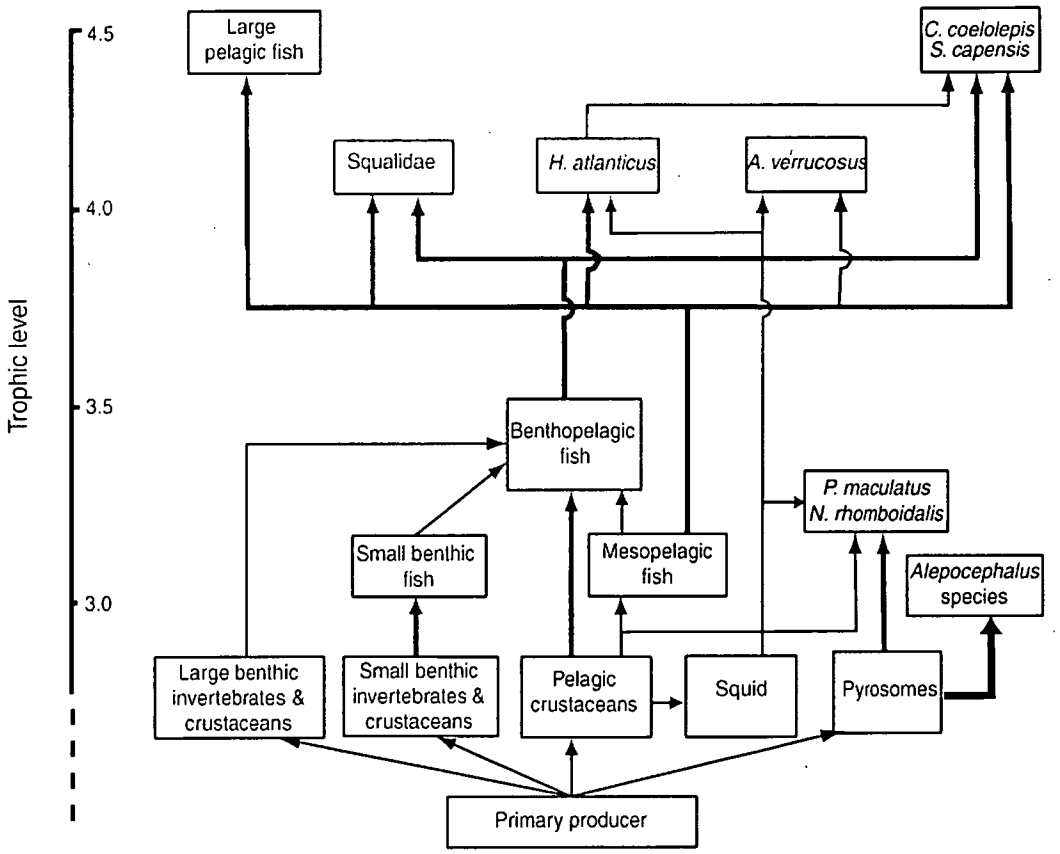


**Fig. 1.** Food web diagram of the major trophic group of the mid-slope community off southern Tasmania (from Bulman et al. in press). Thick lines indicats greater level of contribution. Higher order groups are place by trophic level.

Our models were constructed around the trophic structure of the mid-slope community as described in Bulman *et al.* (2002) (Chapter 3) & Fig 1. We used fishery statistics, survey data and biological data derived from our surveys or from the literature. We investigated the levels of immigration of various trophic groups that would be required to maintain either the flat ground or seamount community compared to the known standing biomass in the overlying water column. Using the time-dynamics Ecosim module, we simulated the effects of fishing on the orange roughy and oreo populations on the seamounts over the decade following their discovery and investigated their rates of recovery, and that of the community generally, in response to changes in fishing pressure.

## Methods

*The study area*

The flat ground study site was located south of Tasmania bounded by 44° 09' S and 147° 04' E, and 44° 13' S and 147° 12' E . The bottom depth in this area was about 1000m and relatively flat compared to the surrounding terrain, which is comprised largely of seamounts. The site was sampled during July 1991, February and November 1992 and April 1993. The area represented by the 'seamount model' was 1111 $km^2$ situated between 145° 37' E to 147°29' E, between the depths 700 and 1200m. This area correlated with two survey areas (N and O) of Bulman *et al.* (1994). It was contained within the Southern Management Zone of the South East Fishery (Tilzey 1994) and all of the orange roughy catch was taken within its bounds. However, the actual area over which the fishing effort was distributed was smaller than the total area, therefore the abundances and catch rates are likely to be conservative. No particular area was defined for the 'flat ground model', but we assumed that it was representative of large portions of the mid-slope in the SEF fishery.

*The Ecopath with Ecosim model*

Christensen and Pauly (1992) developed Ecopath II from the simple steady-state trophic box model originally developed by Polovina (1984), who partitioned the ecosystem into species groups, and given sets of parameters as inputs, produced estimates of mean annual biomass, annual production and annual consumption for each group. This approach was combined with that of Ulanowicz (1986) who analysed flows between components of ecosystems. This software is designed for the basic "construction, parameterization and analysis of mass-balance aquatic and terrestrial ecosystems" (Christensen *et al.* 2000). A further development of this model is the dynamic version, Ecosim, which simulates changes in the ecosystem over time. The construction of these models emphasises ecological relationships rather than mathematical ones (Trites *et al.* 1999) and therefore makes use of data and knowledge routinely kept by biologists.

Detailed descriptions of the Ecopath with Ecosim model and underlying equations can be found in Walters *et al.* (1997) and Christensen *et al.* (2000). The base equation is for a predator *i*:

$$B_i.(P/B)_i..EE_i - \sum_{j=1}^{n} B_j..(Q/B)_j..DC_{ji} - Y_i - E_i - BA_i = 0$$

where $B_i$ is biomass, $P_i$ is production, $EE_i$ is the ecotrophic efficiency or the proportion of production that is used in the system, $n$ is the total number of prey groups $j$, $Q$ is the consumption, $DC_{ji}$ is the fraction of prey $i$ in predator $j$ diet, $Y_i$ is fishery catch, $E_i$ is net migration rate and $BA_i$ is biomass accumulation (Christensen *et al.* 2000). *EE* varies between 0 and 1 and approaches one if the predation pressure is high.

To parameterise the model, three out of four parameters must be provided: biomass, *B*, production/biomass, *P/B*, consumption/biomass, *Q/B*, or ecotrophic efficiency, *EE*. The program then estimates the fourth parameter. Diet composition, catch data, assimilation, migration and biomass accumulation are also required inputs.

*Species groups of the model*

A box in the model can be either a single species or a group of ecologically related species, or a size or age class of a species. The models we describe have 19 groups of which 10 are fish, seven are invertebrates, one is a primary producer, and one is a detritus group (see Table 2 for listing).

The species groupings are based on the assemblages of the trophic food web described by Bulman *et al.* (in press) (Fig. 1) with the additional groups of zooplankton, infauna and detritus. Apart from groups of single species, groups' compositions were as follows. The squalids was represented by *Centroscymnus crepidater*, *C. owstoni*, *Etmopterus granulosus* and *Deania calcea*. The scavengers were *Centroscymnus coelolepis* and *Synaphobranchus capensis,* which were quite different from each other morphologically. The oreo group consisted of *Pseudocyttus maculatus*, *Neocyttus rhomboidalis* and *A. niger*. The pelagic fish group comprised a few large species such as *Macruronus novaezelandiae*, *Macrourus carinatus*, *Tetragonurus cuvieri* and *Tubbia*

*tasmanica.* The benthopelagic fish group included macrourids such as *Coryphaenoides serrulatus, C. subserrulatus, Caelorinchus kermadecus, C. innotabilis* and others such as *Epigonus* species. The only representative of the small benthic fish was taken to be *Caelorinchus kaiyomaru.* Mesopelagic fish included the lanternfish such as *Lampichthys australis, Lampanyctus procerus, Bathylagus antarcticus, Chauliodus sloani, Phosichthys argenteus* and *Serrivomer* sp. The pelagic crustaceans included the larger crustaceans such as the pelagic prawns, e.g., *Acanthephyra* species and mysids, e.g., *Gnathophausia* species. Gelatinous zooplankton comprised salps *Salpa* species and pyrosomes *Pyrosoma atlanticum atlanticum.* The zooplankton group consisted of small zooplankton such as copepods, amphipods, and ostracods. Large epibenthos included large and mobile animals such as large crabs, octopus or large bivalves. Small epibenthos included small sessile crustaceans, molluscs and echinoderms. Infauna was assumed to be mostly polychaetes. Primary producers were considered to be all phytoplankton species. We had no knowledge of fishes' diets on the seamounts and assumed them to be similar to that described by Bulman *et al.* (2002).

*Biomass estimates*

Biomass for scavengers, squalids, warty oreo and other oreos, and alepocephalids were estimated from catch composition data from the four cruises. In each of the cruises, a series of demersal trawls was made over a 24 h period. Tows of between half and one hour duration were made every four hours. The fish caught were identified to species, weighed and counted. Biological samples and data were obtained from selected species for other dietary and metabolic investigations. For each species, abundance per tow was calculated as catch weight per tow divided by the area swept by the net per tow. The mean density or standing biomass of each species was the mean of all tows (Table 1). These estimates were used in the 'flat ground model'.

However, since the abundances of orange roughy, and probably the oreos, on the seamounts, were under-represented by the flat bottom surveys (Koslow *et al.* 1994), the pre-fishing biomass estimate from the stock assessment models for orange roughy, i.e. 89 000-148 000 t ($\bar{x}$ =118 500 t), was used to calculate a density of 106.7 t km$^{-2}$ (Smith & Wayte 2001). Unfortunately there are no estimates of oreo biomass, therefore the estimates from the trawl survey were scaled up by using a scaling factor for orange

roughy calculated from the difference between the abundance estimates from the stock assessments and the trawl survey.

**Table 1. Mean densities of fish species calculated from demersal tows from four surveys of the study area on the mid-slope (about 1000m) off southern Tasmania.**

| Species | Mean density t $km^{-2}$ |
|---|---|
| Deania calcea | 0.0256 |
| *Centroscymnus crepidater* | 0.0791 |
| *C. owstoni* | 0.0196 |
| *C. coelolepis* | 0.0702 |
| *Etmopterus baxteri* | 0.1775 |
| *Synaphobranchus capensis* | 0.2352 |
| *Alepocephalus* sp. 2 | 0.0893 |
| *Alepocephalus* sp. 1 | 0.0968 |
| *Halargyreus johnstonii* | 0.0895 |
| *Macrourus carinata* | 0.0400 |
| *Caelorinchus innotabilis* | 0.0003 |
| *Coryphaenoides serrulatus* | 0.0085 |
| *C. subserrulatus* | 0.0999 |
| *C. kaiyomaru* | 0.0229 |
| *C. kermadecus* | 0.0009 |
| *Hoplostethus atlanticus* | 0.5155 |
| *Neocyttus rhomboidalis* | 0.0084 |
| *Pseudocyttus maculatus* | 0.0115 |
| *Allocyttus verrucosus* | 0.0445 |
| *Allocyttus niger* | 0.0012 |
| *Epigonus lenimen* | 0.0009 |
| *E. robustus* | 0.0054 |
| others | 0.0792 |
| Total | 1.658395 |

Koslow *et al.* (1997) estimated biomass for micronekton, i.e. mesopelagic fishes and crustaceans, using acoustic methods and compared them to those made using trawls by Williams and Koslow (1997). The trawl estimates for the micronekton groups

were also reported in Parslow *et al.*1996, however, the acoustic estimates were considered more accurate so were used in preference where appropriate. Parslow *et al.* (1996) reported estimated biomass for zooplankton and primary producers in g C, and Terauds (1993) estimated zooplankton biomasses, all of which were converted to wet weight, using a general carbon to biomass scaling factor of 14.25 (Jarre-Teichmann *et al.* 1998). The mean values observed were used in the model (see Table 4) except that the model also estimated standing biomass of the primary producers. The observed range was 17 to 71 t wet wt $km^{-2}$ (Parslow *et al.* 1996).

*Diet composition*

The diet compositions of the demersal and large pelagic fishes (Table 2) are based on Bulman *et al.* (2002)(Chapter 3) and those of the mesopelagics were based on Williams *et al.* (in press). Since we had no dietary data for lower trophic groups, we used the data from Jarre-Teichmann *et al.* (1998) and Trites *et al.* (1999), whose species groupings and ecology were most similar to ours.

*P/B and Q/B estimates*

Unless otherwise stated, *P/B* estimates were calculated in Fishbase (Froese and Pauly 2001) using Fishbase data on maximum lengths where necessary and a mean temperature of 5°C, the temperature at 1000m (Parslow *et al.* 1996). *Q/B* was calculated using the relationship of Palomares and Pauly (1999) although it probably overestimates *Q/B* for these deep-sea species. The estimated parameters were compared with those of similar groups from similar studies and were all found to be very conservative, and therefore are probably reasonable estimates for our deep-sea species. However, it is noted that the food conversion ratios are about 10% or lower. This seems appropriate for orange roughy and the oreos since they are very slow-growing and relatively high metabolic rates and high reproduction costs. For the other demersal species, conversion efficencies of about 10-15% were probably appropriate, given the scarcity of food and high energy costs of searching for food.

*P/B* for each species in the Squalidae was calculated using maximum lengths. The average *P/B* for the group was 0.17 and the average *Q/B* was 1.5. The average *P/B*

**Table 2. Diet composition of the species groups used in the Ecopath models of the mid-slope fish communities off southern Tasmania**

| | Prey/Predator | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | Squalids | | | | | | | | | | | | | | | | | |
| 2 | Scavengers | | | | | | | | | | | | | | | | | |
| 3 | Alepocephalids | | | | | | | | | | | | | | | | | |
| 4 | Orange roughy | | | | | | | | | | | | | | | | | |
| 5 | Oreos | | | | | | | | | | | | | | | | | |
| 6 | Warty oreo | | | | | | | | | | | | | | | | | |
| 7 | Pelagic fishes | | 0.308 | | | | | | | | | | | | | | | |
| 8 | Benthopelagic fishes | 0.233 | 0.323 | | 0.205 | 0.005 | | 0.250 | | | | | | | | | | |
| 9 | Small benthic fishes | | | | | | | | 0.068 | | | | | | | | | |
| 10 | Mesopelagic fishes | 0.682 | 0.017 | 0.010 | 0.467 | | 0.529 | 0.250 | 0.104 | 0.018 | | | | | | | | |
| 11 | Squid | 0.037 | 0.016 | | 0.075 | 0.073 | 0.166 | | 0.015 | | | | | | | | | |
| 12 | Large epibenthos | 0.001 | 0.004 | | 0.049 | 0.073 | 0.210 | | 0.232 | 0.087 | | | | | | | | |
| 13 | Gelatinous zooplankton | 0.017 | | 0.987 | 0.009 | 0.791 | 0.014 | 0.501 | 0.020 | | | | | | | | | |
| 14 | Infauna | | | | | | | | 0.010 | 0.435 | | | | | | | | |
| 15 | Small epibenthos | | | 0.002 | 0.010 | | 0.015 | | 0.120 | 0.430 | | | 0.20 | | | | | |
| 16 | Pelagic crustaceans | 0.005 | 0.003 | 0.001 | 0.185 | 0.058 | 0.066 | | 0.430 | 0.030 | 0.80 | 0.90 | | 0.25 | | | | |
| 17 | Zooplankton | | | | | | | | | | 0.20 | 0.10 | | 0.25 | 0.20 | 0.40 | 0.40 | |
| 18 | Primary producers | | | | | | | | | | | | | 0.25 | | | 0.60 | 0.60 |
| 19 | Detritus | 0.025 | 0.329 | | | | | | | | | | 0.80 | 0.25 | 0.80 | 0.60 | | 0.40 |

for the two species of scavengers was 0.145 and the average *Q/B* of the two species was 1.4.

Smith *et al.*1995 reported mortality, *M*, for *H. atlanticus* as 0.048 or 0.064. The lower value was used to approximate *P/B*, and *Q/B* was estimated as 2.0. Since the oreos, including warty oreo, are of similar ages to orange roughy (Stewart *et al.* 1995), it was assumed that *P/B* would be similar. The higher value of 0.06 was used for all oreos. New Zealand stock assessments use an *M* of 0.063 (Doonan et al. 2001) and the von Bertalanffy growth efficient, *k*, of warty oreo was slightly higher than for orange roughy. *Q/B* of 2.2 was used for all oreos.

The average *P/B* of the pelagic fish groups was 0.21 and the average *Q/B* was 2.4. The average *P/B* of the benthopelagic fish group was 0.37 and the average *Q/B* was 3.3. The *P/B* of the only representative of the small benthic group, *C. kaiyomaru,* was estimated to be 0.30 and the *Q/B* was 2.4.

The average *P/B* for slickheads was 0.26 and *Q/B* was 2.1, although these values might be too high for this species.

The average *P/B* of the mesopelagic fishes, calculated at 8° C because they were higher in the water column, was 0.6 and the *Q/B* was 3.7. These values were lower than those of Mendoza (1993), Silvestre *et al.* (1993), Olivieri *et al.* (1993) Jarre-Teichmann *et al.* (1998) and Trites *et al.* (1999).

No data for squid from our region were available so the *P/B* value of 3.2. was based on Trites *et al.* 1999. Values for squid vary between 1.5 in the Benguelan upwelling (Jarre-Teichmann *et al.* 1998) to 5.0 in Monterey Bay (Olivieri *et al.* 1993). *Q/B* was assumed to be 10.7 similar to Trites *et al.* (1999).

For the pelagic crustaceans, a *P/B* of 5.0 was assumed, and *Q/B* of 17 similar Trites *et al.* (1999). Very large differences for these parameters can be found in the literature but these can be accounted for by the difference in definition of the species composition of the zooplankton.

*P/B* for gelatinous zooplankton was estimated at 1.0, slightly higher than those values of Trites *et al.* (1999) and Jarre-Teichmann *et al.* (1998), and lower than

that of Olivieri *et al.* (1993) (0.875, 0.6 and 5 respectively). Our *Q/B* value of 5.0 was slightly higher than that of Trites *et al.* (1999).

For large epibenthos, a *P/B* of 2.5 was similar to other studies with benthos groups comprised of similar taxa. For small epibenthos, we assumed a conservative *P/B* of 2.0, and a *Q/B* of 8. Again, the species composition of the benthos groups will influence the overall estimate of P/B however the values we use fall within the ranges of values for the component taxa. For infauna, a *P/B* of 1.4 and *Q/B* of 6 were assumed, similar to Trites *et al.* (1999).

We used a *P/B* for the zooplankton of 6.0 similar to Trites *et al.* (1999) but several times less than the values of Mendoza *et al.* (1993) and Olivieri *et al.* (1993). *Q/B* was 20.0.

*Immigration rates*

Immigration rates of trophic groups were calculated by entering all four parameters, i.e., *P/B*, *Q/B*, *EE* and *B* and allowing Ecopath to estimate the net migration rates. These rates were then re-entered as immigration rates and the models were rerun. To simulate advection rates for the micronekton and zooplankton groups, these rates were also scaled from 0.5 to 1.5 x base rate. The other groups, benthopelagic fishes and benthic fishes retained the same rate because we assumed they were not affected by advection.

The five levels of immigration rates were used to simulate the response of the whole ecosystem to the scenario of no further fishing following the decade of fishing.

*Fishing scenarios*

The effect of intense fishing on orange roughy and oreos, which occurred from 1990, was simulated by Ecosim to see how the system would respond and if it resembled the current presumed situation for orange roughy. Annual fishing mortality rates, F, for the orange roughy and oreo fisheries during the 10 year period, were calculated from reported catches (Chesson 1996, Smith and Wayte 2000, Wayte

and Bax 2001) and applied to the Ecosim model (Table 3). We explored how the stocks would respond to five scenarios of fishing: (1) if fishing ceased after the initial decade of fishing;(2) if it continued at the last known rate; (3)if it increased by two- and (4) five-fold on roughy but oreo fishing ceased or (5) if it continued at a level equal to the mortality rate (0.048) and oreo fishing also ceased.

**Table 3. Fishing mortality rates, *F*, for oreos and orange roughy calculated from fishery catch statistics and applied to the first 11 years of Ecosim simulations.** Where no data (n.d.) was available for oreos, *F* was set to 0.3. 1990 corresponds to the first year in the model simulation.

| Year | Oreo | Orange roughy |
|---|---|---|
| 1990 | - | 0.21 |
| 1991 | - | 0.12 |
| 1992 | 0.54 | 0.09 |
| 1993 | 0.23 | 0.097 |
| 1994 | 0.28 | 0.059 |
| 1995 | 0.22 | 0.03 |
| 1996 | 0.18 | 0.011 |
| 1997 | 0.6 | 0.0063 |
| 1998 | 1.31 | 0.0035 |
| 1999 | n.d. | 0.0024 |
| 2000 | n.d. | 0.004 |

## Results

The 'flat ground model' was balanced after inputting the biomasses of the top six predator groups. The resulting estimates were consistent with the observed standing biomasses except for benthopelagic and benthic fishes, where estimates were 10-100 times greater than observed (Table 4). This may be because trawl estimates usually underestimate abundances considerably. Apart from those groups,

the model predicted that the flat ground community could be supported by the observed standing biomass.

The 'seamount model' was also initially balanced by providing the biomasses of the top six predators only and allowing Ecopath to estimate the biomasses of the other groups (Table 4). This resulted in a balanced model but with very high standing biomasses of the lower trophic groups, exceeding those observed from the study of Parslow *et al.* (1996). Biomasses of mesopelagic fishes, squid and gelatinous zooplankton were 2 -3 times higher than observed, pelagic crustaceans were 60 times higher and zooplankton and primary producers were nearly 50 times higher. The biomasses of benthopelagic fishes and benthic fishes were over 100 t $km^{-2}$, several orders of magnitude greater than observed. This suggested that much of the production sustaining orange roughy and other top predators in the ecosystem must be sourced from out of the model area, i.e. it was advected into the seamount area from an area upstream of unknown dimensions. The most likely immigrant groups were the micronekton groups of mesopelagic fishes, pelagic crustaceans, gelatinous zooplankton and squid, and the zooplankton. The second model, the seamount migration model, was built by inputting estimated standing biomasses for these pelagic groups, and calculating the net migration for each group necessary to rebalance the model (Table 4). These were then entered as immigration rates.

*System statistics*

Most of the system statistics of the flat ground model were different to those of the seamount non-migration model, accounted for by the vast difference in standing biomass of orange roughy. Consumption, exports, system production and flows were higher in the seamount model (Table 5). The characteristics that did not change such as connectance, were those that are dependent on the underlying structure of the model.

Similarly, most system characteristics of the seamount base migration model were dramatically different to those of the non-migration model (Table 5). Total consumption in the migration model declined to 5% of the non-migration model and consequently respiratory flows also declined. Similarly, the total system throughput of the migration model, which is the sum of all the flows and represents

**Table 4. Parameters of Ecopath models for flat ground and seamounts, off southern Tasmania.** *P/B* = production/biomass, *Q/B*= consumption/biomass. *EE*=ecotrophic efficiency. Biomasses in parentheses are inputs. For the seamount migration model, immigration rates for trophic groups were estimated by inputting their biomass.

| Trophic group | Trophic level | Flat ground model biomass (t $km^{-2}$) | Seamount non-migration model biomass (t $km^{-2}$) | Seamount migration model biomass (t $km^{-2}$) | *P/B* ($y^{-1}$) | *Q/B* ($y^{-1}$) | *EE* | Immi-gration rate (t $km^{-2}$ $y^{-1}$) |
|---|---|---|---|---|---|---|---|---|
| Squalids | 4.3 | (0.3) | (0.3) | (0.3) | 0.17 | 1.5 | 0.00 | - |
| Scavengers | 3.8 | (0.3) | (0.3) | (0.3) | 0.145 | 1.4 | 0.00 | - |
| Alepocephalid: | 3.6 | (0.19) | (0.19) | (0.19) | 0.26 | 2.1 | 0.00 | - |
| Roughy | 4.1 | (0.5) | (106.7) | (106.7) | 0.048 | 2.0 | 0.00 | - |
| Oreos | 3.6 | (0.04) | (4.11) | (4.11) | 0.06 | 2.2 | 0.00 | - |
| Warty dory | 4.0 | (0.08) | (8.21) | (8.21) | 0.06 | 2.2 | 0.00 | - |
| Pelagic fishes | 4.0 | 0.68 | 0.68 | 0.68 | 0.21 | 2.4 | 0.90 | - |
| Benthopelagic fishes | 3.5 | 4.76 | 133.46 | (0.283) | 0.37 | 3.3 | 0.90 | 44.349 |
| Small benthic fishes | 3.3 | 3.96 | 111.03 | (0.03) | 0.30 | 2.4 | 0.90 | 0.055 |
| Mesopelagic fishes | 3.3 | 5.73 | 297.39 | (100) | 0.60 | 3.7 | 0.90 | 56.039 |
| Squid | 3.4 | 0.14 | 10.27 | (5) | 3.20 | 10.7 | 0.80 | 6.901 |
| Large epibenthos | 2.3 | 2.28 | 70.18 | 7.56 | 2.50 | 7.5 | 0.80 | - |
| Gelatinous zooplankton | 2.6 | 2.02 | 24.21 | (6.8) | 1.00 | 5.0 | 0.80 | 5.128 |
| Infauna | 2.2 | 3.83 | 107.46 | 0.036 | 1.40 | 6.0 | 0.80 | - |
| Small epibenthos | 2.4 | 5.88 | 171.97 | 8.69 | 2.00 | 8.0 | 0.80 | - |
| Pelagic crustaceans | 2.4 | 6.98 | 309.2 | (5) | 5.00 | 17.0 | 0.80 | 370.409 |
| Zooplankton | 2.0 | 16.19 | 633.27 | (14) | 6.00 | 20.0 | 0.80 | 81.339 |
| Primary producers | 1.0 | 5.58 | 224.65 | 4.74 | 80.0 | - | 0.60 | - |
| Detritus | 1.0 | | | - | - | - | *0.82 | |

**Table 5. System statistics of the Ecopath models of the mid-slope flat ground and seamount communities.** 'Base' rate is that estimated by the model to balance the system given observed standing biomasses as calculated from the field survey data (Table 1).

| | Flat ground | Seamount | | | | | |
|---|---|---|---|---|---|---|---|
| | | Immigration rate of micronekton | | | | | |
| System statistics | none | none | base x 0.5 | base x 0.75 | base | base x 1.25 | base x 1.5 |
| Sum of all consumption (t $km^{-2}y^{-1}$) | 591.4 | 22735.3 | 1188.4 | 1188.4 | 1188.4 | 1188.4 | 1188.4 |
| Sum of all exports (t $km^{-2}y^{-1}$) | 233.2 | 9849.3 | 5.4 | -124.5 | -254.5 | -384.4 | -514.4 |
| Sum of all respiratory flows (t $km^{-2}y^{-1}$) | 213.4 | 8122.8 | 633.6 | 633.6 | 633.6 | 633.6 | 633.6 |
| Sum of all flows into detritus (t $km^{-2}y^{-1}$) | 425.7 | 16708.2 | 517.7 | 517.7 | 517.7 | 517.7 | 517.7 |
| Total system throughput (t $km^{-2}y^{-1}$) | 1464 | 57416 | 2345 | 2215 | 2085 | 1955 | 1825 |
| Sum of all production (t $km^{-2}y^{-1}$) | 609 | 24309 | 612 | 612 | 612 | 612 | 612 |
| Net primary production (t $km^{-2}y^{-1}$) | 446.6 | 17972.1 | 379.2 | 379.2 | 379.2 | 379.2 | 379.2 |
| Total primary production/total respiration | 2.09 | 2.21 | 0.60 | 0.60 | 0.60 | 0.60 | 0.60 |
| Net system production (t $km^{-2}y^{-1}$) | 233.2 | 9849.3 | -254.5 | -254.5 | -254.5 | -254.5 | -254.5 |
| Total primary production/total biomass | 7.51 | 8.12 | 1.39 | 1.39 | 1.39 | 1.39 | 1.39 |
| Total biomass/total throughput | 0.04 | 0.04 | 0.12 | 0.12 | 0.13 | 0.14 | 0.15 |
| Total biomass (excluding detritus) (t $km^{-2}$) | 59.4 | 2213.6 | 272.6 | 272.6 | 272.6 | 272.6 | 272.6 |
| Connectance Index | 0.216 | 0.216 | 0.216 | 0.216 | 0.216 | 0.216 | 0.216 |
| System Omnivory Index | 0.192 | 0.154 | 0.193 | 0.193 | 0.193 | 0.193 | 0.193 |
| Ascendancy (%) | 25.7 | 26.6 | 49.2 | 29.9 | 33.0 | 18.3 | 17.0 |

the overall size of the system, declined to about 4% of the non-migration model. Total net primary production required fell from nearly 17972 to 379 t $km^{-2}y^{-1}$.

Most interesting was the decline of the ratio of the total primary production to total respiration from 2.213 to 0.60, since this ratio is considered an important

indication of the maturity of the system, according to Odum (Christensen *et al.* 2000). A value exceeding 1 indicates a developing system, while a value approaching 1 indicates maturity.

The net system production went from largely positive to negative, because of the immigration of some groups. Large values indicate 'immature systems' (Christensen *et al.* 2000). Total biomass fell to about a tenth of the non-migration model and the total system biomass that is supported by the available energy flow, the biomass/throughput ratio, trebled from 0.04 to 0.12. This ratio should maximize when a system approaches maturity (Christensen *et al.* 2000).

Primary production/biomass ratio was lowest in the migration model system and 3-4 times higher for the flat ground and non-migration seamount models. In immature systems biomass should accumulate and this ratio should be high (Christensen *et al.* 2000). As the system matures the ratio declines.

The connectance index of the system, i.e. the proportion of actual linkages compared to the potential linkages, indicates complexity of the system. This ratio was 0.216. Complex systems are considered to be more mature. However, this value is dependent on the detail of taxonomy and construction of the model and therefore does not change between the models.

The system omnivory index of the migration model increased from 0.154 to 0.193. This index measures the average omnivory index of all consumers, weighted by the log of their food intake, and is used to determine the extent to which a system displays web-like features (Christensen *et al.* 2000). It is regarded as a better measure of maturity.

Ascendancy is a measure of the average mutual information in a system scaled by throughput (Christensen 1995, Christensen *et al.* 2000). The flat ground model and the seamount non-migration model had similar ascendancies and amongst the lowest. The difference between ascendancy and its upper limit, capacity, is the system overhead. It reflects the system's ability to cope with unexpected perturbations. Christensen (1995) showed that ascendancy was negatively correlated with maturity for 41 systems, and that system overhead was therefore positively

correlated with stability. Imports affect ascendancy and differences in immigration rates were reflected by the differences in ascendancies.

*Fishing scenarios and the effects of immigration rates*

The response of the major trophic groups to 'no further fishing' with three of the five immigration rates are presented in Fig 2; (a) base rate, (b) 0.5 x base rate and (c) 1.5 x base rate. For orange roughy and oreos, response to all levels of migration were investigated by simulating the no further fishing scenario. After 10 years of simulated fishing, the stocks of orange roughy and oreos declined in the base immigration model (Fig 3, Table 6). After 40 years of the 'no further fishing' scenario, the orange roughy and oreos had attained 99% and 57% respectively of their pre-fishing biomasses, and most of the groups had similar biomasses to their pre-fishing ones (Table 6).

**Table 6. Relative changes in biomass of trophic groups after 50 years of Ecosim simulation of the seamount migration model in response to a 'no future fishing' scenario, and five levels of immigration rates of micronekton.**

| | Relative change in biomass | | | | |
|---|---|---|---|---|---|
| | Immigration rate of micronekton | | | | |
| Trophic group | Base x 0.5 | Base x 0.75 | Base x 1 | Base x 1.25 | Base x 1.5 |
| Squalids | 0.70 | 0.87 | 1.04 | 1.22 | 1.39 |
| Scavengers | 1.37 | 1.35 | 1.37 | 1.41 | 1.46 |
| Alepocephalids | 2.29 | 2.39 | 2.49 | 2.59 | 2.69 |
| Roughy | 0.63 | 0.81 | 0.99 | 1.18 | 1.37 |
| Oreos | 0.32 | 0.44 | 0.57 | 0.72 | 0.88 |
| Warty oreo | 0.63 | 0.88 | 1.11 | 1.33 | 1.55 |
| Pelagic fishes | 1.42 | 1.47 | 1.54 | 1.60 | 1.67 |
| Benthopelagic fishes | 1.30 | 1.12 | 1.01 | 0.93 | 0.87 |
| Small benthic fishes | 0.55 | 0.77 | 0.98 | 1.19 | 1.38 |
| Mesopelagic fishes | 0.58 | 0.79 | 0.99 | 1.19 | 1.39 |
| Squid | 0.55 | 0.78 | 1.00 | 1.22 | 1.43 |
| Large epibenthos | 0.99 | 0.98 | 0.99 | 1.02 | 1.07 |
| Gelatinous zooplankton | 1.17 | 1.25 | 1.32 | 1.40 | 1.49 |
| Infauna | 1.10 | 1.03 | 0.99 | 0.99 | 1.02 |
| Small epibenthos | 0.71 | 0.85 | 0.98 | 1.10 | 1.22 |
| Pelagic crustaceans | 0.62 | 0.82 | 1.00 | 1.16 | 1.32 |
| Zooplankton | 0.92 | 0.95 | 0.99 | 1.03 | 1.07 |
| Primary producers | 1.15 | 1.07 | 1.00 | 0.94 | 0.89 |

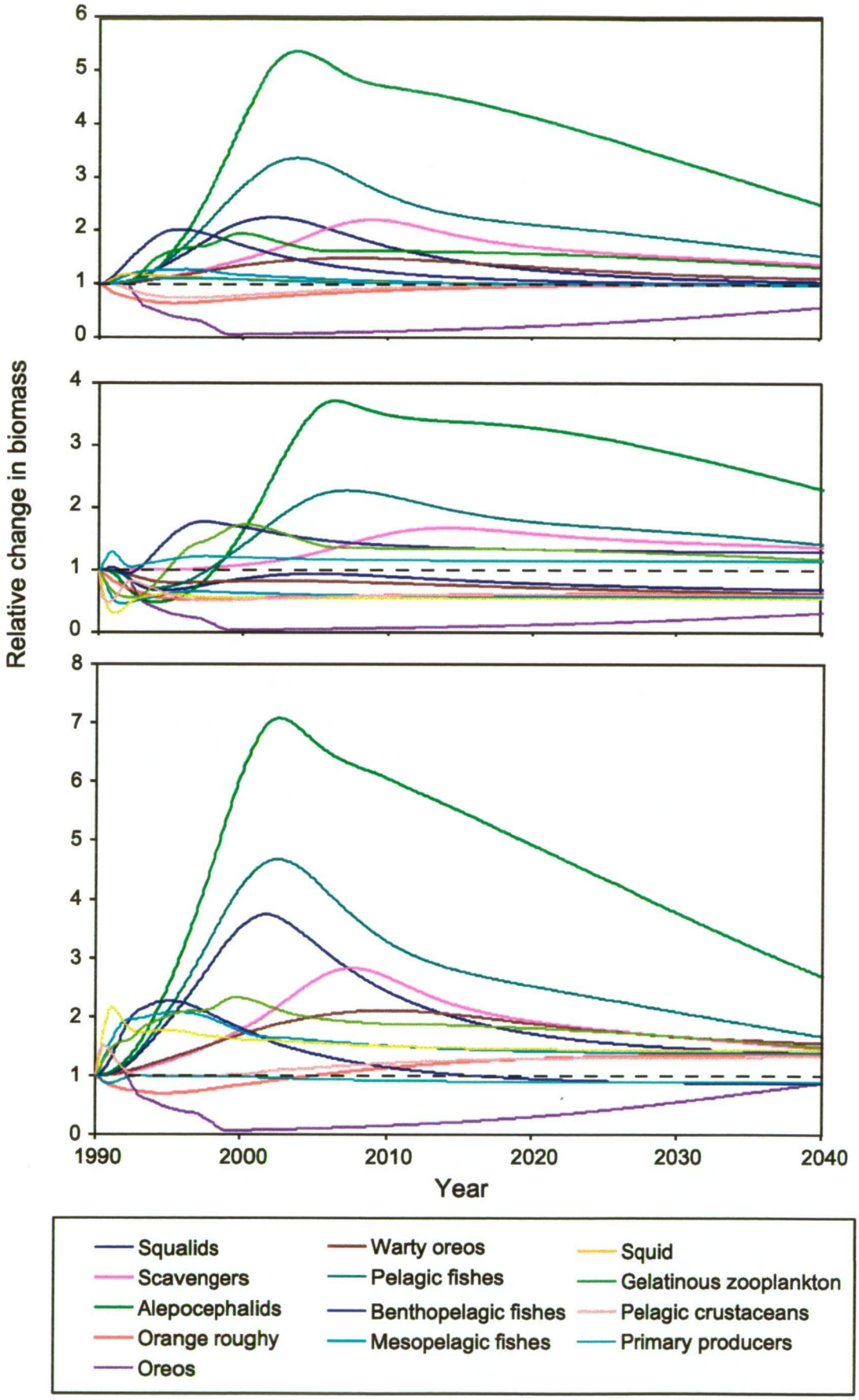


**Fig. 2.** Comparison of change in biomass of selected trophic groups over 50 years of Ecosim simulations in response to 'no future fishing' and three levels of immigration rates of micronekton: (a) 'base' x1 (b) base x 0.5 (c) base x 1.5.

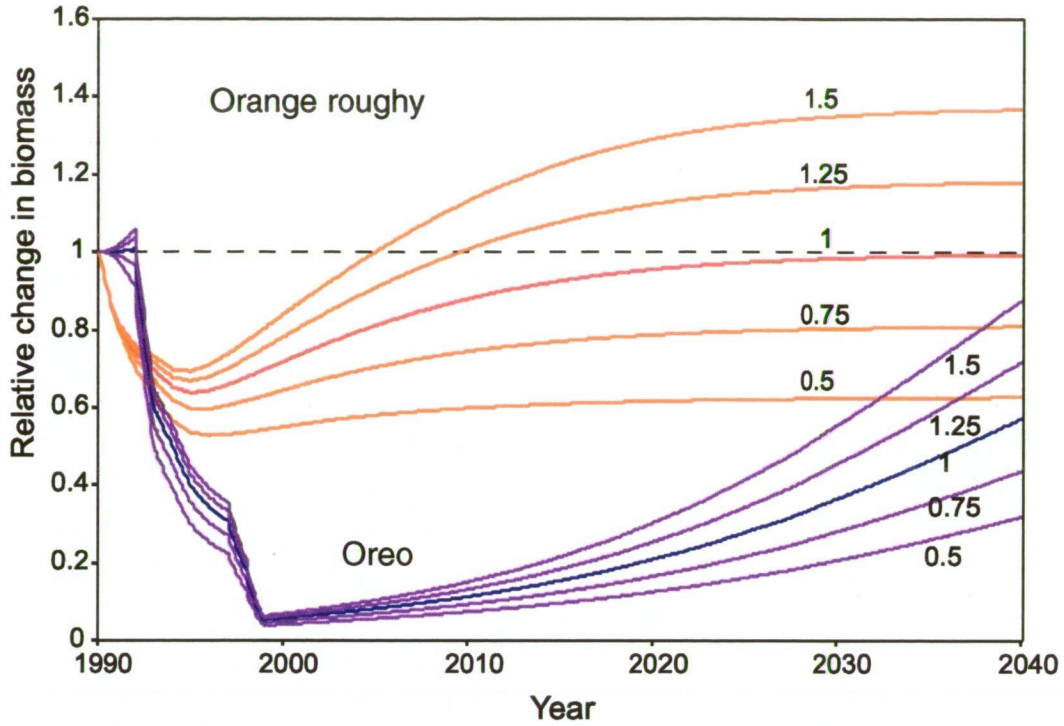


**Fig 3.** Relative change in biomass of orange roughy and oreos after 50 years of Ecosim simulations of the 'no future fishing" scenario and five levels of immigration.

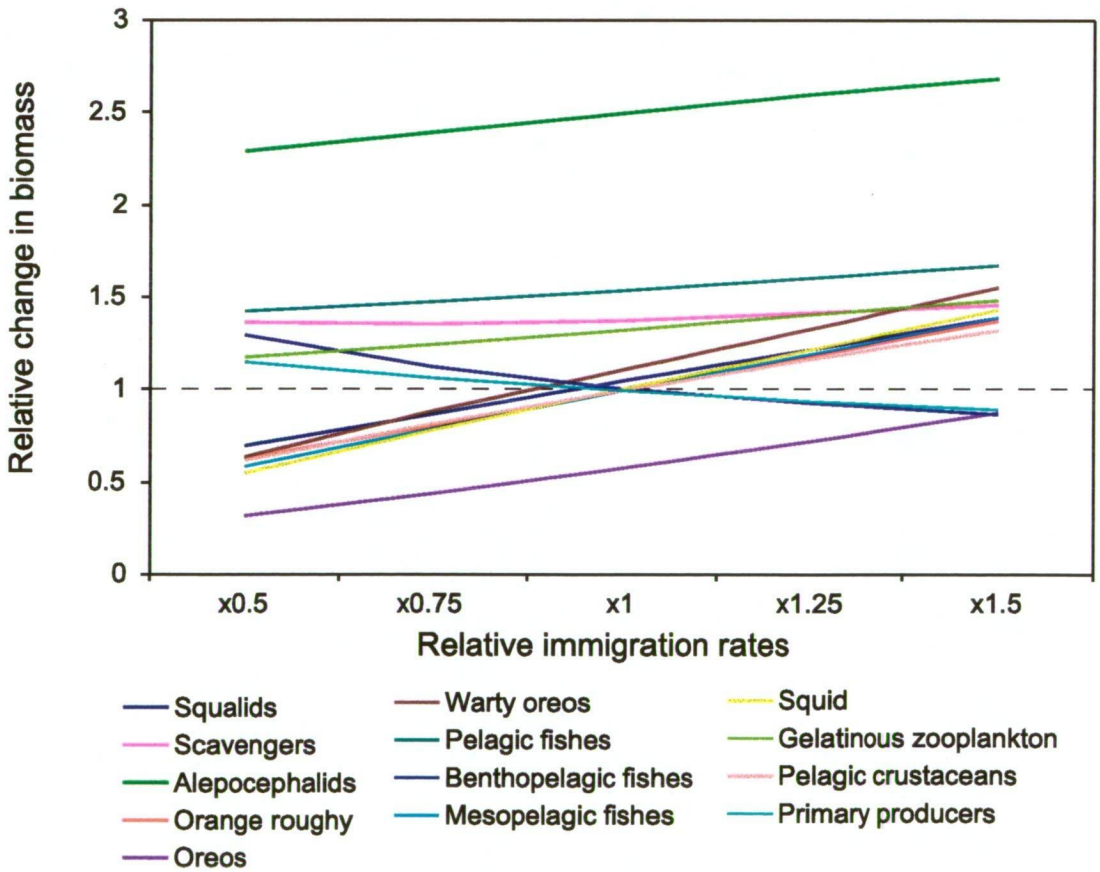


**Fig. 4.** Relative changes in biomass of selected trophic groups after 50 years of Ecosim simulation of the 'No future fishing' scenario and five levels of immigration rates of micronekton.

Some species such as the alepocephalids, scavengers and pelagic fishes had increased but would return to pre-fishing levels if the model were run beyond 40 years. However if the immigration rates of the micronekton groups were increased or decreased the responses changed (Fig 2b, c). The effects of fishing on oreos and roughy were very pronounced in the simulation. Roughy stocks recovered in less than 20 years at higher immigration rates (Fig 3). However, if immigration rates were halved, roughy stayed at about 60% of pre-fishing even after 100 years. The effect on oreos was even more dramatic (Fig 3). Oreos recovered more slowly than orange roughy if resources were available, but the effect of reduced resources had less impact on them than it did on orange roughy, and their rate of recovery was greater. The ratios of the final biomass to the initial biomass of fish groups (Table 6) increased in response to variations in immigration rates of the micronekton groups (Fig 4).

At the base level of migration, the effect of future fishing at various rates produced predictable results for the stocks. The highest fishing mortality on roughy of 0.048 caused a continual decline of the roughy stocks (Table 7, Fig 5). A five-fold increase in fishing rate to 0.02, which is still quite low, would suppress the stocks to about 80% pre-fishing biomass. However current or doubled rates would allow gradual recovery of the stock in just over 40 years, but it must be noted that these rates are very low. Continued fishing on oreos at their current level of exploitation resulted in their collapse only 10 years later. However, these predictions for oreos are based on uncertain standing biomass estimates and are therefore indicative only.

**Table 7. Future fishing scenarios, their fishing rates, and relative changes in biomass of orange roughy and oreo after 50 years of Ecosim simulation of the seamount migration model at the base migration rate.**

| | Fishing rate | | Relative biomass | |
|---|---|---|---|---|
| **Future fishing scenario for 2001-2040** | **Orange roughy** | **Oreo** | **Orange roughy** | **Oreo** |
| No fishing | - | - | 0.99 | 0.57 |
| Current | 0.004 | 0.3 | 0.96 | 0 |
| Double | 0.008 | - | 0.92 | 0.59 |
| Fx5 | 0.02 | - | 0.79 | 0.62 |
| F x 0.048 | 0.048 | - | 0.48 | 0.56 |

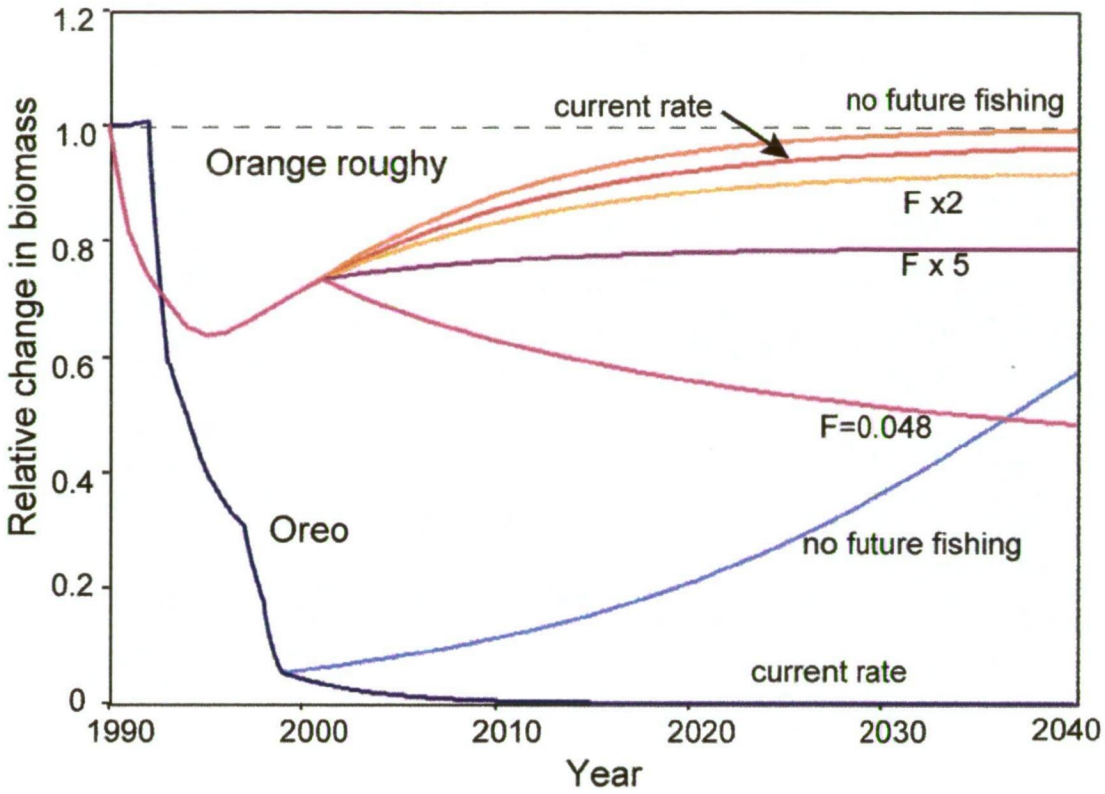


**Fig. 5.** Relative changes in biomass of orange roughy and oreos after 50 years of Ecosim simulation of the various rates of continued fishing scenarios and the base level of immigration rate of micronekton.

## Discussion

This model is one of the first attempts to model a deep-water fishery using the Ecopath with Ecosim software. This approach produces a mass-balanced model, useful in exploring the way in which the system is structured and how it functions (Ware 1990). Christensen (1998) used Ecopath to investigate responses to fishery pressures of the heavily exploited ecosystem of the Gulf of Thailand. He constructed two mass-balanced models to describe the fishery, at two different phases of its development, and used Ecosim to predict the ecosystem-level changes leading from the initial phase to the later phase. Trites *et al.* (1999) similarly developed two EwE models to describe the Bering Sea ecosystem in the 1950s before commercial fishing, and in the 1980s after marine mammal populations had declined. Bundy

(2001) investigates the cause of the collapse of Atlantic cod stocks, and the decline of other demersal stocks, on the east coast of Canada. The Ecopath model was used to simulate a variety of responses of the Newfoundland-Labrador ecosystem to predation and fishing, under a variety of assumptions of control. Recently, an EwE model was developed to describe eastern shelf area of the South East Fishery off southeastern Australia with particular reference to the local seal population dynamics (Goldsworthy *et al.* in press). The model was developed from trophic investigations of the demersal fishes of the shelf fishery (Bulman *et al.* 2001). Goldsworthy *et al.* (in press) showed that marine mammals were major consumers on the shelf, and played an important part in structuring the food web.

Bundy (2001) also explored the implications of top-down vs. bottom-up control on the cod fishery collapse and decline of plaice and yellowtail flounder. Being a trophodynamic model, it was not always able to correctly predict all trends of all groups because of its inability to directly account for other causes of mortality (Bundy 2001). Our models have assumed a 'mixed control', neither top-down nor bottom-up. The effect of changing the vulnerability of prey to predation might be a useful future development for the mid-slope community models, particularly if the two models could be combined in a spatial framework, as in Ecospace (Walters et al.1997).

Moving the mass-balanced Ecopath model dynamically away from equilibrium is also considered a weakness of Ecosim (Walters *et al.* 1997) and may have accounted for some failures of prediction (Bundy 2001). However, the EwE model predictions were generally consistent with the theory of the collapse of the cod fishery in the region. Pitcher (2001) described some short-comings of the Ecopath suite of models (some of which are being addressed) but concluded that their strength was their ability to analyse system-wide responses to fishing, as well as suitability for continual development. While all models have their limitations, this type of model provides a significant step towards understanding the structure and function of the mid-slope demersal fish community and the seamount fishery for orange roughy.

Our seamount fishery is not unique either as a seamount, or as a deep-sea fishery. Deep-sea fishes have been exploited in the North Atlantic since the 1950s and by the1970s great fleets of modern ocean-going trawlers were 'mining' these

fisheries world-wide until their eventual collapse (Merrett and Haedrich 1997). Between 1967 and 1975, the pelagic armorhead *Pseudopentaceros wheeleri* on the North Pacific seamounts were fished by Soviet and Japanese fleets (Boehlert and Genin 1987). About a million tonnes were taken but the high catch rates, not surprisingly, declined dramatically in the later years. Like other deep-sea fisheries, this one could not sustain the high exploitation rates because of slow growth and low recruitment of the species. Boehlert and Genin (1987), in their review of the interactions of biological processes and seamounts, suggested that the high standing stocks of exploitable fishes were maintained on the seamounts by high rates of energy transfer, either advected or in situ.

The hypothesis that the aggregating stocks of orange roughy on the seamounts are supported from external sources was supported by the Ecopath and Ecosim results. The net production of 17972 t $km^{-2}$ $y^{-1}$ required to sustain the system in the non-migration model, is about 6 times higher than the estimated primary production in the area (2850 t $km^{-2}$ $y^{-1}$; estimated from 200g C $y^{-1}$ (Parslow *et al.* 1996)). The net primary production required for the base migration model of 379 t $km^{-2}$ $y^{-1}$ (Table 5), is less than the field estimate. We did not try to match the model estimate of annual primary production to the field estimate by altering migration rates because of the uncertainty of treating some groups, such as the benthopelagic fishes, as migratory or non-migratory. In our model we treated them as migratory because the standing biomass estimated from the surveys was very low and the system required a greater biomass to balance consumption of them by their predators. Their ecology and life history suggest that they are probably not migratory and certainly are not similar to the advected groups. Trial runs of our model, treating benthopelagic and benthic fishes as non-migratory, and allowing the model to predict their standing biomass, resulted in a model estimate of primary production similar to the field estimate. However, different treatment of these groups had little effect on the recovery rates of orange roughy and oreos. Nevertheless the implication is that maintenance of the seamount system requires an additional input of resources.

On the flat ground, the overall primary production required to support the system, regardless of origin and not accounting for migration, was only about 450 t $km^{-2}$ $y^{-1}$ (Table 5) and therefore still supportable by local production.

Koslow (1997) calculated that, given an ecological transfer efficiency of 10%, only about 2 g C of the 200 g C $m^{-2}$ $y^{-1}$ primary production would be available to the fourth trophic level in which orange roughy reside. He calculated that, given a population density for orange roughy of 5 t C $km^{-2}$ (or about 100 t wet wt $km^{-2}$, similar to our biomass estimates), and the consumption rate of 1% body weight per day (Bulman & Koslow 1992), orange roughy alone required 9-23 t C $km^{-2}$ $y^{-1}$, or about 10 times more than available. Our consumption estimates for orange roughy from the Ecopath model were similar. Total annual consumption by roughy was 213 t $km^{-2}$ or about 15 g C $m^{-2}$, accounting for nearly 90% of the total consumption of the top predators (Table 8). However, on the flat ground the consumption of orange roughy is only 1 t $km^{-2}$ $y^{-1}$ or 0.07 t C $km^{-2}$ $y^{-1}$, about 40% of the total consumption of top predators and less then the available 2 t C $km^{-2}$ $y^{-1}$. This result supports Koslow's (1997) calculation that local production could sustain non-aggregated populations of orange roughy and other fishes on the flat grounds.

The longevity of orange roughy on the mid-slope, and their low production, suggests that this ecosystem is an old or mature one. However, maturity of an ecosystem is not easily defined and has not been done so satisfactorily (Christensen 1995). The system characteristics that we examined from Odum's range of characteristics attributable to mature systems were less than conclusive in their diagnosis. Our system is probably much smaller than the system to which the original concept was applied, and would account for the inconclusive results. The migration model, which modelled advection of the pelagic trophic groups, generally resulted in a more "mature" system according to Odum's characteristics, or ,by implication, a more stable one (Christensen 1995, Vasconcellos *et al.* 1997). However, maturity does not ensure stability or resilience against perturbations. Walters and Holling (1990) demonstrated that even unmanaged systems are characterized by periods of instability and unexpected shifts in behaviour due either to external or internal causes. Life histories and biology of species such as orange roughy and the oreos make them extremely vulnerable to exploitation, a major perturbation by most definitions.

The real attraction of the dynamic models is their ability to explore the behaviour of the ecosystem over time. The Ecosim model was also able to produce a feasible, although conservative, replication of the effects of fishing on the orange roughy. Allowing for growth, the simulated decline in orange roughy stocks reached

**Table 8. Consumption (t $km^{-2}y^{-1}$) of trophic groups of mid-slope community estimated by the seamount migration model.**

| | Prey \ Predator | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | Squalids | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| 2 | Scavengers | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| 3 | Alepocephalid | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| 4 | Roughy | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| 5 | Oreos | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| 6 | Warty dory | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| 7 | Pelagic fishes | - | 0.129 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| 8 | Benthopelagic fishes | 0.11 | 0.136 | - | 43.75 | 0.05 | - | 0.41 | - | - | - | - | - | - | - | - | - | - |
| 9 | Small benthic fishes | - | - | - | - | - | - | - | 0.06 | - | - | - | - | - | - | - | - | - |
| 10 | Mesopelagic fishes | 0.3 | 0.007 | 0.004 | 99.66 | - | 9.56 | 0.41 | 0.10 | 0.001 | - | - | - | - | - | - | - | - |
| 11 | Squid | 0.02 | 0.007 | - | 16.01 | 0.66 | 3.00 | - | 0.01 | - | - | - | - | - | - | - | - | - |
| 12 | Large epibenthos | tr | 0.002 | - | 10.46 | 0.66 | 3.80 | - | 0.22 | 0.006 | - | - | - | - | - | - | - | - |
| 13 | Gelatinous zooplankton | 0.01 | - | 0.394 | 1.92 | 7.15 | 0.25 | 0.82 | 0.02 | - | - | - | - | - | - | - | - | - |
| 14 | Infauna | - | - | - | - | - | - | - | 0.01 | 0.031 | - | - | - | - | - | - | - | - |
| 15 | Small epibenthos | - | - | 0.001 | 2.13 | - | 0.27 | - | 0.11 | 0.031 | - | - | 11.35 | - | - | - | - | - |
| 16 | Pelagic crustaceans | 0.002 | 0.001 | tr | 39.48 | 0.52 | 1.19 | - | 0.40 | 0.002 | 292.16 | 48.14 | - | 8.5 | - | - | - | - |
| 17 | Zooplankton | - | - | - | - | - | - | - | - | - | 72.84 | 5.36 | - | 8.5 | 0.04 | 27.8 | 34.0 | - |
| 18 | Primary producers | - | - | - | - | - | - | - | - | - | - | - | - | 8.5 | - | - | 51.0 | 168.0 |
| 19 | Detritus | 0.01 | 0.138 | - | - | - | - | - | - | - | - | - | 45.41 | 8.5 | 0.18 | 41.7 | - | 112.0 |
| | Sum | 0.45 | 0.420 | 0.399 | 213.40 | 9.04 | 18.06 | 1.64 | 0.93 | 0.072 | 365.00 | 53.50 | 56.76 | 34.0 | 0.22 | 69.5 | 85.0 | 280.0 |

about 60 % of pre-fishing biomass, about 20 % greater than the result of subtracting the total catches from the pre-fishing biomass. Given the same mortality rate, current stock assessments predict a high probability that the stocks are less than 30% pre-fishing biomass (Wayte and Bax 2001).

However, the model estimates are sensitive to initial biomass estimates and parameters and our model could be improved by increasing the accuracy of these parameters. The orange roughy pre-fishing biomass estimates were probably reasonable being based on stock assessments that have been constantly and rigorously scrutinised, but we do not have the same confidence in the oreo estimates. The calculation of fishing rate, $F$, is affected by initial biomass and the response to fishing could be over- or underestimated. The predictions of response of the either of the stocks to future fishing regimes should be regarded with caution as any prediction. However, the ways, or directions, in which the stocks respond to perturbations, are probably a reasonable indication, given the uncertainty in the parameters.

Parameters for which better estimates might improve our model, are mortality rates, prey vulnerability and immigration or advection rates of prey groups Another discrepancy was that the model estimates of biomass for benthopelagic and benthic fish groups were much higher than those of the field survey. However, the consumption of these groups by the top predators including roughy, dictated that a far greater abundance was required to support them than was apparently available.

Models are limited by how the key ecosystem components are parameterised (Ware 1990). How the structure is developed and the elements of the groups are important. Groups could be broad, consisting of a number of species, or very specialised, consisting of a stage of the life cycle of a specific species, e.g. juveniles or adults. The life history parameters that describe the groups could be quite difficult to estimate in the case of a group of species with very different biology and ecology. For instance, the scavenger group is comprised of two quite different fishes that were grouped on functional criteria in the food web analysis. This assessment might not be appropriate if the life history parameters of the species are very different. As more groups are defined, the more complex the model becomes and the larger and more difficult the task of quantifying the parameters becomes.

However, the overwhelming dominance of orange roughy might render more precision irrelevant.

With increasing pressure on fisheries management to develop ecologically sustainable fisheries, generally of a multi-species nature, fisheries research has to find ways to provide information about the ecology of the fished communities. The trophic models developed here is are examples of an approach which provides a relatively simple framework, but is capable of accounting for the major components and trophic interactions, predicting changes over time and producing results consistent with ecological theory (Vasconcellos *et al.* (1997).

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## References


**Boehlert, G. W. and Genin, A.** (1987). A review of the effects of seamounts on biological processes. pp 319-334. *In* Keating, B. H.(ed). 'Seamounts, Island and Atolls' (American Geophysical Union: Washington, D.C.)

**Bulman, C. M., Wayte, S. E. and Elliott, N.G.** (1994), Orange roughy surveys, 1988 and 1989; Part A, Abundance Indices; Part B, Biological data. *CSIRO Marine Laboratories Report* **215**: 21 pp.

**Bulman, C., Althaus, F., He, X., Bax, N. and Williams, A.** (2001). Diets and trophic guilds of demersal fishes of the south-eastern Australian shelf. *Marine and Freshwater Research* **52**:537-548.

**Bulman, C. M., He, X., and Koslow, J. A.** (2002). Trophic ecology of the mid-slope demersal fish community off southern Tasmania, Australia. *Marine and Freshwater Research* **53**: 59-72.

**Bulman, C. M., and Koslow, J. A.** (1992). Diet and food consumption of a deep-sea fish, orange roughy, *Hoplostethus atlanticus* (Pisces: Trachichthyidae), off southeastern Australia. *Marine Ecology Progress Series* **82**: 115-129.

**Bundy, A.** (2001). Fishing on ecosystems: the interplay of fishing and predation in Newfoundland-Labrador. *Canadian Journal of Fisheries and Aquatic Science* **58**:1153-1167.

**Chesson, J.** (ed) (1996). 'The South East Fishery 1995.' Fishery Assessment Report compiled by the South East Fishery Assessment Group. (Australian Fisheries Management Authority: Canberra.)

**Christensen, V.** (1995). A model of trophic interactions in the North Sea in 1981, the Year of the Stomach. *Dana* **11**: 1-28.

**Christensen, V.** (1998). Fishery-induced changes in a marine ecosystem: insight from models of the Gulf of Thailand. *Journal of Fish Biology* **53A**:128-142.

**Christensen, V. and Pauly, D.** (1992). The Ecopath II – a software for balancing steady-state ecosystem models and calculating network statistics. *Ecological Modelling* **61**: 169-185.

**Christensen, V. and Pauly, D.** (1993). On steady-state modelling of ecosystems. *In* Christensen, V. and Pauly, D. (eds). 'Trophic models of aquatic ecosystems'. ICLARM Conference Proceedings 26. pp.14-19.

**Christensen, V., Walters, C. J. and Pauly, D.** (2000). Ecopath with Ecosim: a User's Guide, October 2000 edition. (Fisheries Centre, University of British Columbia, Vancouver, Canada and ICLARM, Penang, Malaysia.)

**Doonan, I. J., McMillan, P. J., Coburn, R. P. and Hart, A.C.** (2001). Assessment of OEO4 smooth oreo for 2000-01. New Zealand Fisheries Assessment Report 2001/21. 37 pp.

**Genin, A., Haury, L., and Greenblatt, P.** (1988). Interactions of migrating zooplankton with shallow topography: predation by rockfishes and intensification of patchiness. *Deep-Sea Research* **35**: 151-175.

**Goldsworthy, S., Bulman, C., He, X., Larcombe, J. and Littnan, C.** (in press). Trophic interactions between marine mammals and Australian fisheries: an ecosystem approach. *In* Gales, N., Hindell, M. and Kirkwood, R. (Eds) 'Marine Mammals and Humans: towards a sustainable balance.' (University of Melbourne Press: Melbourne.)

**Froese, R. and Pauly, D.** (2001). (Eds) FishBase. ICLARM, Manila, Philipines. (www.fishbase.org)

**Isaacs, J. D., and Schwartzlose, R. A.** (1965). Migrant sound scatterers: interaction with the sea floor. *Science* **150**: 1810-1813.

**Jarre-Teichmann, A., Shannon, L. J., Moloney, C. L. and Wickens, P. A.** (1998). Comparing trophic flows in the southern Benguela to those in other upwelling ecosystems. *South African Journal of Marine Science* **19**: 392-414.

**Koslow, J. A., Bulman, C. M., and Lyle, J. M.** (1994). The mid-slope demersal fish community off southeastern Australia. *Deep-Sea Research* **41**: 113-141.

**Koslow, J. A.** (1997). Seamounts and the ecology of deep-sea fisheries. *American Scientist* **85**: 168-176.

**Koslow, J. A., Kloser, R. J. and Williams, A.** (1997). Pelagic biomass and community structure over the mid-continental slope off southeastern Australia based upon acoustic and midwater trawl sampling. *Marine Ecology Progress Series* **146**: 21-35.

**Mendoza, J. J.** (1993). A preliminary biomass budget for the northeastern Venezuela shelf ecosystem. *In* Christensen, V. and Pauly, D. (eds). 'Trophic models of aquatic ecosystems'. ICLARM Conference Proceedings 26. pp 285-297.

**Merrett, N. R., and Haedrich, R. L.** (1997). 'Deep-Sea Demersal Fish and Fisheries.' (Chapman & Hall: London.)

**Olivieri, R. A., Cohen, A. and Chavez, F. P.** (1993). An ecosystem model of Monterey Bay, California. *In* Christensen, V. and Pauly, D. (eds). 'Trophic models of aquatic ecosystems'. ICLARM Conference Proceedings 26. Pp 315-322.

**Palomares, M. L. D. and Pauly, D.** (1989). A multiple regression model for predicting the food consumption of marine fish populations. *Australian Journal of Marine and Freshwater Research* **40**: 259-273.

**Parslow, J., Koslow, J. A., Griffiths, F.B., Clementson, L., Rathbone, C., Bonham, P., and McKenzie, D.** (1996). 'Tasmanian slope trophodynamics: Final report to FRDC Project 91/17.' (CSIRO Division of Fisheries: Hobart, Tasmania.) 160 pp.

**Pauly, D., Christensen, V. and Walters, C.** (2000). Ecopath, Ecosim, and Ecospace as stools for evaluating ecosystem impact of fisheries. *ICES Journal of Marine Science* **57**: 697-706.

**Pereyra, W.T., Pearcy, W. G. and Carvey, F.E.** (1969). *Sebastodes flavidus*, a shelf rockfish feeding on mesopelagic fauna, with consideration of the ecological implications. *Journal of the Fisheries Research Board of Canada* **26**: 2211-2215.

**Pitcher, T. J.** (2001). Fisheries managed to rebuild ecosystems? Reconstructing the past to salvage the future. *Ecological Applications* **11**: 601-617.

**Polovina, J. J.** (1984). Model of a coral reef ecosystem I. The Ecopath model and its application of French Frigate Shoals. *Coral Reefs* **3**: 1-11.

**Silvestre, G., Selvanathan, S. and Salleh, A. H. M.** (1993). Preliminary trophic model of the coastal fisheries resources of Brunei Darussalam, South China Sea. *In* Christensen, V. and Pauly, D. (eds). 'Trophic models of aquatic ecosystems'. ICLARM Conference Proceedings 26. Pp 300-306.

**Smith, D.C., Fenton, G. E., Robertson, S. G., and Short, S. A.**(1995). Age determination and growth of orange roughy (*Hoplostethus atlanticus*): a comparison of annulus counts with radiometric ageing. *Canadian Journal of Fisheries and Aquatic Sciences* **52**: 391-401.

**Smith, A.D. and Wayte, S.E.** (eds) (2000). 'The South East Fishery 1999.' Fishery Assessment Report compiled by the South East Fishery Assessment Group. (Australian Fisheries Management Authority: Canberra.)

**Smith, A.D. and Wayte, S.E.** (eds) (2001). 'The South East Fishery 2000.' Fishery Assessment Report compiled by the South East Fishery Assessment Group. (Australian Fisheries Management Authority: Canberra.)

**Stewart, B. D., Fenton, G. E., Smith, D. C. and Short, S. A.** (1995). Validation of otolith-increment age estimates for a deepwater fish species, the warty oreo Allocyttus verrucosus, by radiometric analysis. *Marine Biology* **123**: 29-38.

**Terauds, A.** (1993). Zooplankton on the Southern Ocean mid-slope: vertical distribution and transfer of energy. Dept of Zoology B. Sc. (Hons.) Thesis, University of Tasmania, Hobart, Tasmania.

**Tilzey, R. D. J.** (1994). 'The South East Fishery'. (Bureau of Resource Sciences: Canberra, Australia.) 360 pp.

**Tseitlin, V. B.** (1985). Energetics of fish populations inhabiting seamounts. *Oceanology* **25**: 237-239.

**Trites, A.W., Livingston, P.A., Mackinson, S., Vasconcellos, M.C., Springer, A.M., and Pauly, D.** (1999). Ecosystem change and the decline of marine mammals in the eastern Bering Sea: testing the ecosystem shift and commercial whaling hypothesis. *Fisheries Centre Research Report* Vol.**7**.

**Ulanowiscz, R.E.** (1986).Growth and development: ecosystem phenomenology. (Springer-Verlag: New York.)

**Vasconcellos, M., Mackinson, S., Sloman, K. and Pauly, D.** (1997). The stability of trophic mass-balance models of marine ecosystems: a comparative analysis. *Ecological Modelling* **100**: 125-134.

**Vinogradov, M. E., and Tseitlin, V. B.** (1983). Deep-sea pelagic domain (Aspects of bioenergetics). In 'Deep Sea Biology.' The Sea, Vol 8. (Ed. G. T. Rowe.) pp.123-165. (John Wiley & Sons: New York.)

**Walters, C., Christensen, V. and Pauly, D** (1997). Structuring dynamic models of exploited ecosystems from trophic-mass-balance assessments. *Reviews in Fish Biology and Fisheries* **7**: 139-172.

**Walters, C., Pauly, D. and Christensen, V.** (2000). Ecospace: prediction of mesoscale spatial patterns in trophic relationships of exploited ecosystems, with emphasis on the impacts of marine protected areas. *Ecosystems* **2**: 539-554.

**Walters, C. J. and Holling, C. S.** (1990). Large-scale management experiments and learning by doing. *Ecology* **71**: 2060-2068.

**Ware, D. M.** (1990). Aquatic ecosystems: Properties and Methods. pp 161-194. *In* 'Fisheries Oceanography'.

**Wayte, S. and Bax, N.** (2001). Orange Roughy (*Hoplostethus atlanticus*). Stock Assessment Report 2001 compiled for the South East Fishery Stock Assessment Group. (Australian Fisheries Management Authority: Canberra.)

**Williams, A., and Koslow, J. A.** (1997). Species composition, biomass and vertical distribution of micronekton over the mid-slope region off southern Tasmania, Australia. *Marine Biology* **130**: 259-276.

**Williams, A., Koslow, J. A., Terauds, A. and Haskard, K.** (in press). Feeding ecology of five fishes from the mid-slope micronekton community off southern Tasmania. *Marine Biology.*

# CHAPTER 6

## Summary

## Summary

Studies of trophic ecology in the deep-sea are challenging, not only because of the physical environment, but because there are presently no methods for studying feeding and energetics of the species, such as might be available in shallow waters or the laboratory. The physical environment of deep-sea causes not only a physical impediment to data collection, but also a financial one. Furthermore, the cost of data collection must be accounted for in time and effort, as well as money. Consequently, deep-sea ecology is a poorly investigated, yet fascinating, area of research.

In this thesis, I present the results of my investigations of the trophic ecology and food web dynamics of the demersal fish community on the mid-slope off southern Tasmania. The lack of knowledge about this community was highlighted when a commercially viable resource of orange roughy, a dominant species in the community, was discovered on the slope. The subsequent discovery of an even larger resource on the seamounts of southern and eastern Tasmania was followed by its inevitable exploitation. Oreos also became commercial targets as the orange roughy catches diminished but even less was known of them. With little knowledge of any of these species at the time, effective management of the fishery was impossible. Since then a great deal of information has gradually accumulated, some of which is presented here.

My investigations of this community have included applications of a wide range of ecological methods, from diet analysis, metabolic estimates using enzyme activities, to construction of food web models, and simulation of impacts of fishing rates and pelagic advection on the food webs. My success in constructing the food web models comes from incorporation of data accumulated from years of research effort in multiple disciplines. The results of this study have provided insights into trophic ecology and energetics of the mid-slope fish community, particularly those of orange roughy. Methods developed in this study can be applied in studying other deep-sea fishes. More significantly, the development of the food web models will

allow further investigations into the system responses to perturbations, such as different fishing regimes, and to natural variability.

During 10 research cruises around southeastern Australia, more than 9000 stomachs from orange roughy and 23 other species were collected for diet analyses. The top predators in the community were orange roughy, the oreos and squalids. Orange roughy is dominant on the flat ground but even more so on the seamounts where densities are more than a hundred times greater.

The majority of prey organisms eaten by the top predators are of a pelagic origin, some of which are advected into the area from adjacent deep-water masses or become available through diel migration from upper layers. The benthopelagic omnivores and piscivores, such as orange roughy, warty oreos and squalids, ate predominantly mesopelagic and benthopelagic fish, crustaceans and squid as adults. In contrast, smooth oreos, alepocephalids and some large pelagic species, ate mostly pyrosomes. The macrourids displayed a variety of trophic modes, but mostly were benthopelagic.

Diet of roughy changed significantly with depth, geographical area and year suggesting that they were opportunistic feeders, reliant on organisms being swept along. Resource partitioning between juveniles and adults was suggested by the patterns of prey selection, a finding that might be useful in restructuring the model in future developments.

The metabolic activity of orange roughy was relatively high for a deep-sea fish. It has relatively high rates of food consumption—adult orange roughy eat 1.15% of their body weight per day—but exceptionally low growth rates. Metabolic activity was similar to those of active, migratory mesopelagic fishes, and substantially higher than those of non-migratory mesopelagic fishes. Also, the proximate bodily composition of orange roughy was similar to that of active mesopelagic fishes rather than the non-migrators.

Direct measurement of metabolism of orange roughy, and the metabolism of seven other dominant species, by measurement of oxygen consumption for example, was impossible for these deep-sea species. However, enzyme activities of white muscle provide good indicators of oxygen consumption, so lactate dehydrogenase (LDH), malate dehydrogenase (MDH) & citrate synthase (CS) activities from the white muscle of the eight species were assayed. Orange roughy, smooth oreo and dogfish had LDH activities higher than the majority of deep-living species studied previously. The oxygen consumption rate for orange roughy estimated from the dietary studies was best approximated from LDH activity. Oxygen consumption for the group of seamount-associated fish to which orange roughy belongs, including the oreos, might also be best estimated by LDH activities. Therefore, these species probably all have relatively high metabolic rates and require a significant energy input to maintain them.

The demersal community on the flat ground could be sustained by the field estimate of primary production, but the seamount population could not, according to the Ecopath model. This supported the hypothesis that advection of additional resources is the most likely mechanism by which the seamount ecosystem is maintained. Advection rates were simulated by estimating the immigration rates of the micronekton groups that were necessary to support the survey estimates of standing biomasses of demersal fishes.

The simulated decline of orange roughy to about 60% of the pre-fishing biomass was based on actual fishing rates for roughy. The stock recovered slowly over the next 40 years once fishing had ceased. The simulated decline for oreos was more dramatic, but they also recovered once fishing ceased. The rate of recovery of both stocks depended on the amount of micronekton immigration. The biomass of pelagic species, particularly the pyrosome feeders, increased substantially but under the base level of immigration of micronekton, including pyrosomes, the ecosystem returned to pre-fishing levels in about 80 years.

Orange roughy and oreos are clearly susceptible to over-fishing. Their life history characteristics of longevity, low production and low fecundity of course make them vulnerable to exploitation. Similarly, other deep-sea fisheries around the world are, or were in some cases, just as vulnerable to over-exploitation. Many stocks have declined or collapsed over the past few decades. The model predictions that the orange roughy and oreo fishery could recover under low levels of fishing was encouraging, but it occurred over a time-span that would be considered by commercial fishers to be uneconomic.

Models are sensitive to data inputs and structure so results from the simulations developed in this study should be viewed with caution. Multi-species fisheries have not been successfully managed to date, but this investigation might provide a useful tool to assist in their management and assessment. Improvement of the models might be possible with more, or better, data for particular groups, such as the benthos or large pelagic fish component, or by adding more structure to the model by splitting key species into juvenile and adult groups. A spatial dimension would be particularly interesting, whereby habitats could be dealt with in one model rather than building several. This development, offered in the Ecospace module, could be useful in assessment of potential marine protected areas. It could be used to explore either the attributes necessary for a successful refuge area, such as the size of source area, or the effects of the refuge on the ecosystem directly, on its surrounds or on fishery catches. A section of the Southern Zone was declared a Marine Protected Area in 2000, and development of our model might be useful in assessing its effectiveness or to explore possible management scenarios.